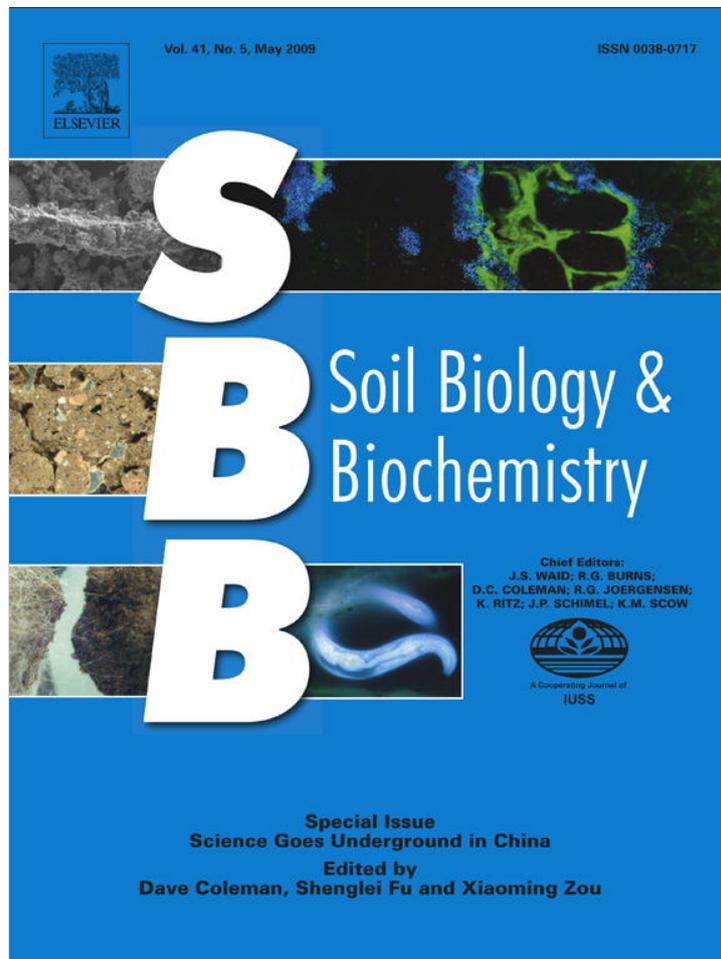


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Soil respiration associated with forest succession in subtropical forests in Dinghushan Biosphere Reserve

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ABSTRACT

This paper reports the results of soil respiration (SR, including heterotrophic and autotrophic respiration), in a presumably successional series (early, middle and advanced) of subtropical forests in Dinghushan Biosphere Reserve in Guangdong Province, China. A static chamber method was used to characterize SR in dynamics of diurnal and seasonal patterns. The relationships of SR with soil temperature (ST) at 5 cm depth and with soil moisture (SM) at 0–10 cm depth were studied in order to estimate the annual SR of each of the forests. The annual SR in a climax forest community, monsoon evergreen broad-leaved forest (MEBF) was estimated as $1163.0 \text{ g C m}^{-2} \text{ year}^{-1}$ and in its successional communities, coniferous and broad-leaved mixed forest (MF) and the Masson pine forest (MPF) were $592.1 \text{ g C m}^{-2} \text{ year}^{-1}$, $1023.7 \text{ g C m}^{-2} \text{ year}^{-1}$, respectively. In addition, removal of surface litter led to the reduction of annual SR by 27–45% in those three forests. Analysis of the results indicated that the annual SR was highly correlated with both ST and SM. Furthermore, ST and SM themselves were highly correlated with each other across season in this study area. Thus for seasonal predictive SR model, either ST or SM could be integrated. However, for SR daily change prediction, both ST and SM were required because of confounding effects of ST and SM on a diurnal time scale. The Q_{10} values of SR derived from ST dependence function were 2.37, 2.31 and 2.25 in the three forests: MPF, MF and MEBF, respectively, suggesting a decreasing trend of the Q_{10} with the degree of forest succession.

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1. Introduction

Forests play a critical role in global terrestrial ecosystems, including providing a temporary carbon sink in the global carbon cycle (Goodale et al., 2002; Zhou et al., 2006), preserving biodiversity (Dobson et al., 1997; Sheil, 2001) and conserving soil and water resources (Woo et al., 1997; Zhou and Yan, 2000). Thus, carbon storage in forests is a key factor in the maintenance of the atmosphere carbon balance. Carbon fluxes in forest ecosystems are dominated by (i) biochemical fixation of CO_2 via plant photosynthesis and (ii) biochemical release of CO_2 via ecosystem respiration (Black, 1973). Soil respiration (SR), a major component of forest ecosystem respiration, is affected seasonally by a variety of environmental factors such as soil temperature (ST), soil moisture (SM), and soil surface litter (Jenkinson et al., 1991; Schlesinger and Andrews, 2000; Grace, 2004; Davidson et al., 2006).

Forest succession is a fundamental ecological process which can modify biogeochemical cycles (Bakker et al., 1997; De Kovel et al.,

2000), ameliorate stand conditions and microclimate factors (Yan et al., 2007) and change in species composition and abundance (Sheil, 2001). The controlling factors compounded in SR are altered during the forest succession (Raich and Tufekcioglu, 2000). The rate of surface litter decomposition is higher in older successional stages of tropical dry secondary forest (Tolosa et al., 2003). Soil organic carbon, total nitrogen and microbial biomass carbon increase quickly with secondary forest succession (Jia et al., 2005). Soil carbon and nitrogen mineralization are related to forest type and age (Cote et al., 2000). The soluble organic carbon and nitrogen fractions increase faster than total soil carbon and nitrogen during forest succession (Banning et al., 2008). Soil carbon, nitrogen and microbe in the secondary forest succession and rehabilitation chronosequence have been studied (Thuille et al., 2002). However, the SR changes along with a forest successional gradient, especially along the natural forest successional gradient, have not been reported.

In the subtropical region, stand composition generally changes from coniferous to coniferous and broad-leaved mixed to broad-leaved in the process of forest succession (Peng and Wang, 1995). A regional forest community, subtropical monsoon evergreen broad-leaved forest (MEBF), as well as its prophase succession communities, coniferous and broad-leaved mixed forest (MF) and

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coniferous Masson pine forest (MPF) have been well reserved at Dinghushan Biosphere Reserve. These systems provide an excellent opportunity for studies of SR alternations along with the natural forest successional gradient. China's subtropical zone is significantly affected by monsoon from the western Pacific and north Indian Oceans (Kong et al., 1997). Generally, high temperature occurs simultaneously with high moisture, so ST and SM are correlated in term of month (Zhou and Yan, 2001). SR is highly correlated with ST and SM (Schlentner and Van Cleve, 1985; Hanson et al., 1993; Davidson et al., 1998; Drewitt et al., 2002; Irvine and Law, 2002). SR generally increases exponentially with ST (Peterjohn et al., 1994; Boone et al., 1998; Moren and Lindroth, 2000), conversely, its relationship with SM is more complex and often determined with site-specific soil parameters (Howard and Howard, 1993). Therefore, it is interesting to examine how SR is altered along with the natural forest successional gradient, for which ST and SM is correlated with each other in the subtropical region.

The objectives of this study are to: (1) investigate the diurnal and seasonal variation of SR in the subtropical forests; (2) focus on the effects of ST and SM on SR under the positive correlation between ST and SM in the subtropical region; (3) quantify the annual SR in the three subtropical forests; (4) test the hypothesis that SR increases during the forest succession.

2. Materials and methods

2.1. Description of field sites

Dinghushan Biosphere Reserve locates 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 and with an area of 1133 ha. Its elevation ranges from 10 to 1000 m above sea level. The terrain is quite hilly with an altitude varying from 100 to 700 m in most areas. The bedrocks of Dinghushan are sandstone and shale belonging to the Devonian Period. The soil profile is mainly lateritic, belonging to the lateritic red soil. The reserve has a subtropical monsoon humid climate with an annual average temperature of 20.9 °C. The highest monthly mean temperature is 28.0 °C in July and the lowest at 12 °C in January. The extreme high and low temperatures are 38 °C and –0.2 °C, respectively. The annual average rainfall is 1956 mm, of which, 80% occurs in the period from May to September, creating a clear wet season and dry season. The annual average relative humidity is 82%.

In the Reserve, there are three types of natural vegetation community (Table 1): MEBF, MF and MPF with age of more than 400, 100 and 50 years, respectively. They represent a sequence of successional stages from climax to pioneer vegetation communities (Peng and Wang, 1995; Kong et al., 1997). The flora includes 260 families, 864 genera, and 1740 species of wild plants and further 349 species of cultivated plants.

2.2. SR, ST and SM measurements

Six plots were randomly located within each forest type, and a permanent chamber base was pushed 5 cm deep into the soil at least 4 weeks before the first sampling and was covered with a chamber and sealed during measurements (Jia et al., 2006). All surface litter (Table 1) was removed from three of the six plots in each forest to identify the effect of litter on SR. 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 sample tube was connected to the upper part of the chamber. Two small electric fans were installed inside the chamber for air mixing. During measurements, the chamber was sealed by filling water into the base'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 from each chamber for laboratory analysis during each measurement. Hourly SR was measured for each plot between 9:00 and 12:00 h once per week and 24-hourly SR was measured once per month. All measurements reported here were conducted from March 2003 to April 2004.

Samples were analyzed for CO₂ concentration using an HP4890D gas chromatograph (Agilent, Wilmington, DE, USA) equipped with flame ionization detectors (FID). CO₂ fluxes were calculated from the rate of change in concentration in the chamber during the sampling interval, determined by linear regression based on five samples. All the coefficients of determination (r^2) of the linear regression were greater than 0.98 in the present study.

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

2.3. Statistical analysis

An exponential function was established to describe the relationship between SR and ST at 5 cm depth:

$$SR = a \exp^{b \cdot ST} \quad (1)$$

where **a** and **b** are fitting parameters: **a** is the base SR and **b** is related to **Q₁₀**, the factor by which a reaction increases for an increase of 10 °C in ST.

A Gaussian function (2) was used to model the relationship between SR and SM at 0–10 cm depth:

$$SR = a_1 \exp^{-0.5 \left(\frac{SM - c}{b_1} \right)^2} \quad (2)$$

where a_1 , b_1 and c are fitted parameters.

Table 1

Some characteristics of the study sites. Soil pH, litter, litterfall and LAI were measured once per month from March 2003 to April 2004.

Stand type	Elevation (m)	Stand age (year)	Soil pH value ^a	Litter (g m ⁻²)	Litterfall (g m ⁻² a ⁻¹)	LAI	Dominant species
MPF	200–300	50–60	3.92 ± 0.03	1058 ± 121	598.3 ± 56.1	4.3 ± 0.4	<i>Pinus massoniana</i> , <i>Rhodomyrtus tomentosa</i> , <i>Ficus variolosa</i> , <i>Baeca frutescens</i> , <i>Blechnum orientale</i> , <i>Schizoloma ensifolium</i>
MF	220–300	About 110	3.86 ± 0.03	686 ± 96	701.2 ± 83.8	6.5 ± 0.7	<i>Pinus massoniana</i> , <i>Schima superba</i> , <i>Castanopsis chinensis</i> , <i>Psychotria rubra</i> , <i>E. variolosa</i> , <i>Evodia lepta</i> , <i>Gahnia tristis</i> , <i>Adiantum capillus-veneris</i>
MEBF	220–300	About 400	3.79 ± 0.05	575 ± 77	893.2 ± 59.2	7.8 ± 0.5	<i>C. chinensis</i> , <i>S. superba</i> , <i>Cryptocarya concinna</i> , <i>Machilus chinensis</i> , <i>Cryptocarya chinensis</i> , <i>Blastus cochinchinensis</i> , <i>Psychotria rubra</i> , <i>Hemigramma decurrens</i>

LAI represents leaf area index. MPF, Masson pine forest; MF, mixed forest; MEBF, monsoon evergreen broad-leaf forest.

^a Soil pH measured in H₂O.

Analysis of variance (ANOVA) was performed to test the significance of differences in SR between forest stands or litter treatments at the $\alpha = 0.05$ level.

3. Results

3.1. Diurnal (24 h) variation of SR

In the Dinghushan area, May, August, November and February are typical months of Spring, Summer, Autumn and Winter seasons, respectively. Seasonal variation in SR may therefore be assessed by comparing the diurnal (24 h) measurements of SR in these months for the three forest types as shown in Fig. 1. Highest rates for three forest types all occurred in August with the litter cover and diurnal variations in the range 3.6–5.0, 3.4–5.9 and 2.0–2.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for MEBF, MF and MPF, respectively. With the litter removed, the diurnal variation ranged from 1.9 to 3.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for MEBF, 1.5–2.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for MF and 1.6–1.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for MPF. Lowest rates were in February without the litter cover when the diurnal variation ranged from 1.5 to 2.0, 1.0 to 1.2 and 0.5 to 0.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for MEBF, MF and MPF, respectively. With the litter cover retained, the diurnal variation ranged from 1.9 to 2.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for MEBF, 1.2–1.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for MF and 0.7–1.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for MPF. Although ST varied significantly through the day in all forest types and all seasons (Fig. 2), no significant differences in SR between day-time and night-time were observed in the present study.

Analysis of the diurnal SR data revealed that the average values from 9:00 to 12:00 were close to the daily means (Fig. 3). We found

that the physical factors such as ST and SM from 9:00 to 12:00, which explain most of the variation in SR at the forest floor (Borken et al., 2002), were also similar to the diurnal mean values, as depicted in Fig. 3. The data used are from May 2003 to April 2004, recorded by the flux station near the MF experimental site. For both ST and SM, the average values from 9:00 to 12:00 are virtually equal to the daily mean values.

3.2. Seasonal dynamics of SR

By assuming that morning measurements of SR (9:00–12:00) were reasonable estimates of the daily mean. We calculated the monthly values of SR as mean SR on the 5 observation days each month, and applied them to further investigate seasonal variation in SR as shown in Fig. 4.

As seen in the comparison of daily data, SR increased with the progress of the succession stages. The annual average SR without the litter cover in MPF, MF and MEBF were 1.1, 1.5 and 2.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. On plots with the litter retained the values were higher, respectively 1.6, 2.7 and 3.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$. We therefore calculated annual SR in MEBF was 1163.0 $\text{g C m}^{-2} \text{year}^{-1}$ and in its succession communities, MF and MPF were 592.1 $\text{g C m}^{-2} \text{year}^{-1}$, 1023.7 $\text{g C m}^{-2} \text{year}^{-1}$, respectively. Removal of surface litter reduced the values of annual SR by 27–45% for the three forests.

The pattern of seasonal variation was the same for every forest type, that is the SR was higher in the wet season than those in the dry season. The values without the litter cover in the wet season were 71.9, 70.4 and 66.5% of the annual total of MPF, MF and MEBF,

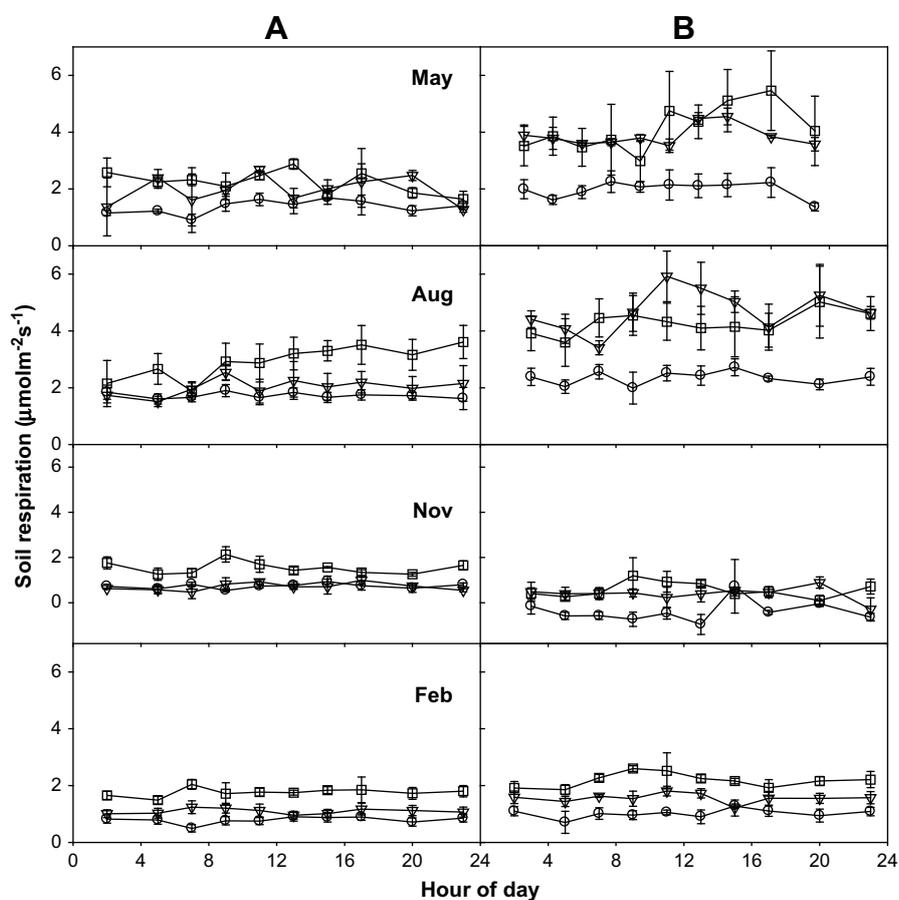


Fig. 1. Diurnal variation of the rate of soil respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) without litter cover (A) and the rate of soil respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) with litter cover (B) in different seasons for three succession forest types. The symbols used are circles, Masson pine forest; triangles, mixed forest; and squares, monsoon evergreen broad-leaved forest.

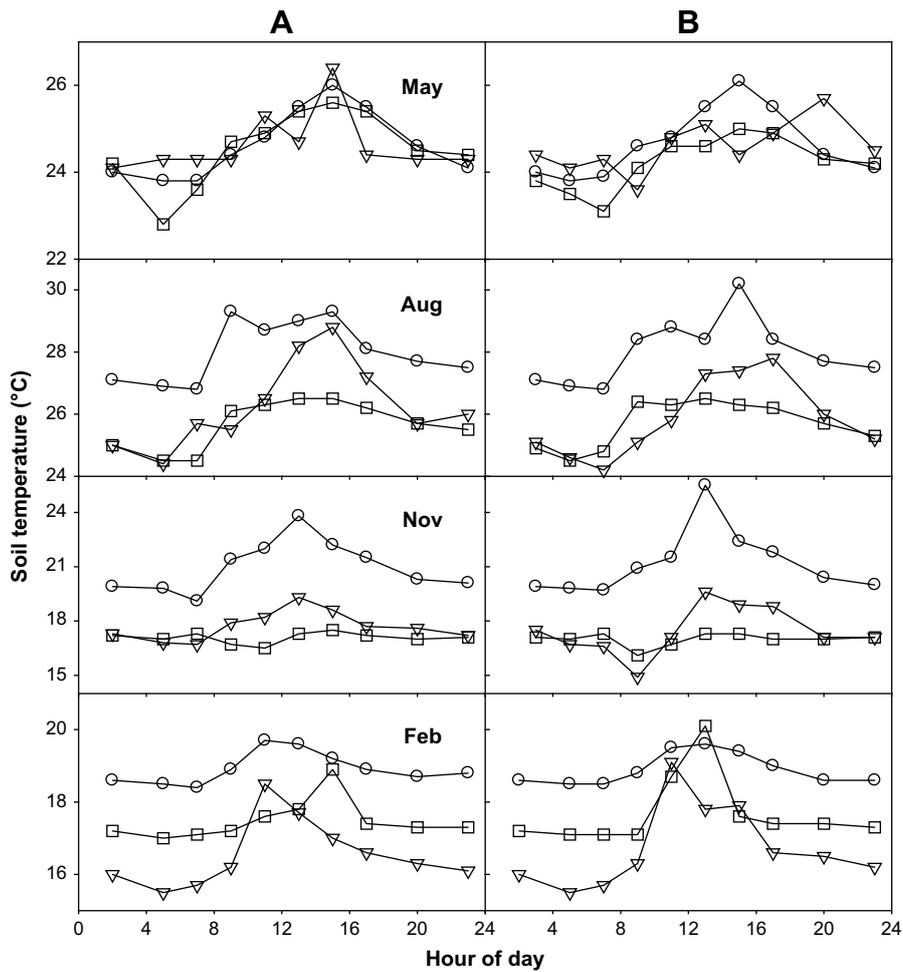


Fig. 2. Diurnal variation of soil temperature (°C) at 5 cm depth without litter cover (A) and soil temperature (°C) at 5 cm depth with litter cover (B) in different seasons for three succession forest types. The symbols used are circles, Masson pine forest; triangles, mixed forest; and squares, monsoon evergreen broad-leaved forest.

respectively. Similarly, the SR with the litter cover in the wet season contributed 73.0, 70.9 and 68.8% of the annual totals of MPF, MF and MEBF, respectively. Therefore, the wet season is critical for C release to the atmosphere from the Dinghushan forest stands.

The SR without the litter cover was 72.0% of that with the litter cover in MPF, 54.9% in MF and 73.2% in MEBF. The percentage figures show that the litter cover had the most significant effect on SR in MF and had a smaller effect in MPF and MEBF.

3.3. Effect of ST on SR

A relationship was established between SR and ST at 5 cm depth. Values of *a* and *b* in function (1) for each forest are shown in Table 2 together with *r*, the correlation coefficient describing the fit of the relationship to the observations. From the values of *r*, we found that they were fairly well described by an exponential relationship with ST (Fig. 5). The regression (1) explained more than 70% of the total

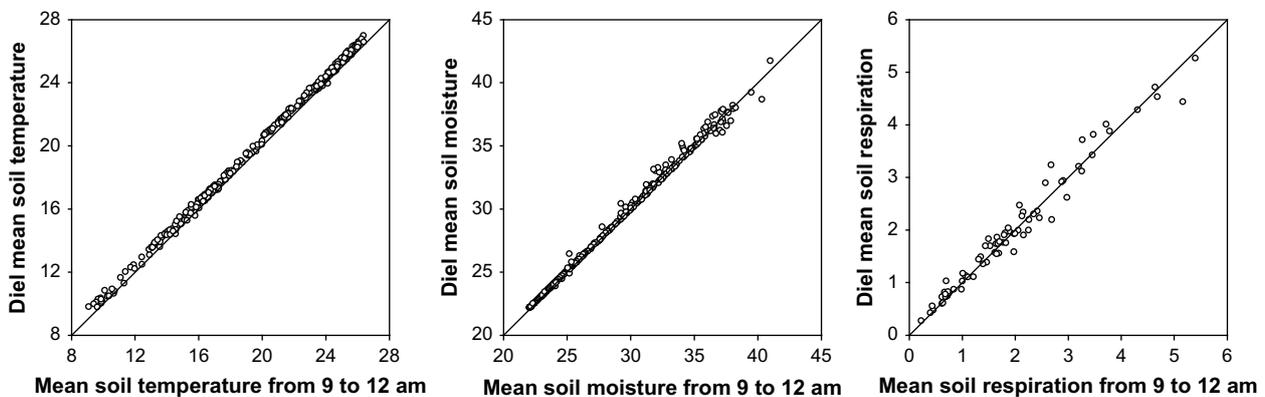


Fig. 3. A comparison of the mean hourly soil temperature (°C) at 5 cm depth, volumetric soil moisture (%) at 0–10 cm depth and the rate of soil respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) from 9:00 to 12:00 h with the 24-hourly diel mean soil temperature (°C) at 5 cm depth, volumetric soil moisture (%) at 0–10 cm depth and the rate of soil respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) in the same days. Note that the solid line is the 1:1 line.

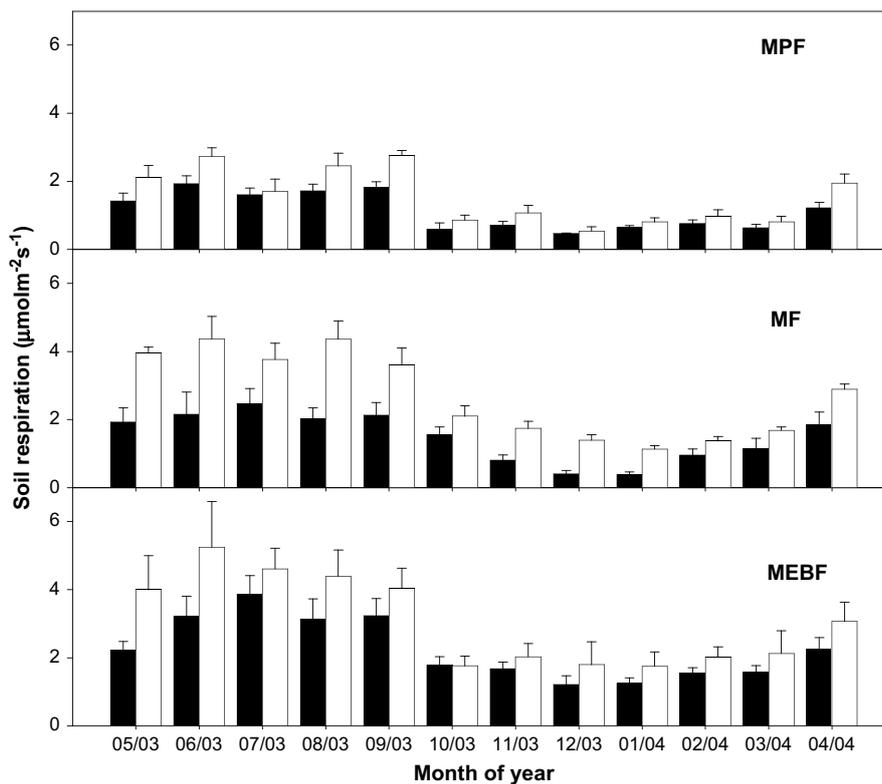


Fig. 4. Monthly dynamics of the rate of soil respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) without litter cover (solid bar) and the rate of soil respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) with litter cover (empty bar) for three succession forest types. MPF, Masson pine forest; MF, mixed forest; MEBF, monsoon evergreen broad-leaved forest.

variation in the measured mean SR over a period of 12 months for all six treatments. We also found the differences of **a** and **b** among the three forest types: **a** increased with forest succession and **b** decreased with forest succession. Both regression coefficients are well within the ranges of values reported for other forests (Raich and Schlesinger, 1992). We can conclude that the predicted SR at the same ST is the lowest for MPF and the highest for MEBF. This result supports that soil microbial activity also increases as forest succession progresses toward the local climax vegetation in the region (Yi et al., 2003).

3.4. Effect of SM on SR

The fitted parameters in function (2) were listed for each treatment in Table 3 together with corresponding values of r_1 , the correlation coefficient. Table 3 showed the fitted relationships between SR and SM. SR had a positive correlation with SM at low SM values, but at high SM, SR tended to plateau or decrease with increasing SM (Fig. 5). The derived functions explained 70–85% of the variation in SR as a function of SM. The values of r_1^2 are similar to the corresponding r^2 values using Eq. (1) for all treatments, that is,

Table 2

Values of regression coefficients (*a* and *b*) in $\text{SR} = a \exp(b \text{ST})$ and correlation coefficient (*r*), where ST is soil temperature at 5 cm depth in °C and SR is soil respiration in $\mu\text{mol m}^{-2} \text{s}^{-1}$. MPF, Masson pine forest; MF, mixed forest; MEBF, monsoon evergreen broad-leaf forest.

Forest type	Soil respiration without litter cover			Soil respiration with litter cover		
	<i>a</i>	<i>b</i>	<i>r</i>	<i>a</i>	<i>b</i>	<i>r</i>
MPF	0.1497	0.0863	0.84	0.2129	0.0862	0.77
MF	0.1961	0.0858	0.83	0.4453	0.0837	0.84
MEBF	0.3827	0.0813	0.82	0.8043	0.0811	0.82

both ST and SM are approximately equally effective as predictors of SR using functions (1) and (2). Because the climate in Dinghushan region has wet (April–September) and dry seasons (October–March), air temperature was higher in the wet season than that in the dry season, so monthly ST and SM in this region were positively correlated. Including SM as a second independent variable together with ST is therefore unlikely to lead to a significant increase in r^2 as compared with using Eq. (1) alone for all treatments. The classic function ($\text{SR} = k \exp^{\beta_1 \text{ST}} \exp^{\beta_2 \text{SM}}$) combined ST and SM together as described by Lloyd and Taylor (1994) was used in this study and explained 62–76% of the temporal variation in SR in the three forests. This figure was lower than those calculated from ST or SM dependence function alone. Thus a model combined ST and SM together was unlikely to improve significantly on the predictive power of the simple ST model in function (1) in this study.

When we measured SR, SM naturally changed with different ST to some degrees. We made no attempt to control SM at the same level or optimum condition with different ST. Hence, the values of parameters in Table 2 represent ST dependence of SR under naturally varying SM conditions. As a test of this conclusion, we examined the relation between SM and the residuals from the ST model (function (1)) for the MEBF forest type (Fig. 6). A positive relationship was found between the residuals and SM for plots both with and without the litter cover. However, the degree of scatter in the plotted points suggests that the trends were as expected.

4. Discussion

4.1. Temporal variation in SR

The daily curves for all three forest types were relatively flat in November and February, during the dry season (October to March). Stronger diurnal variation was apparent in MF and MEBF in May

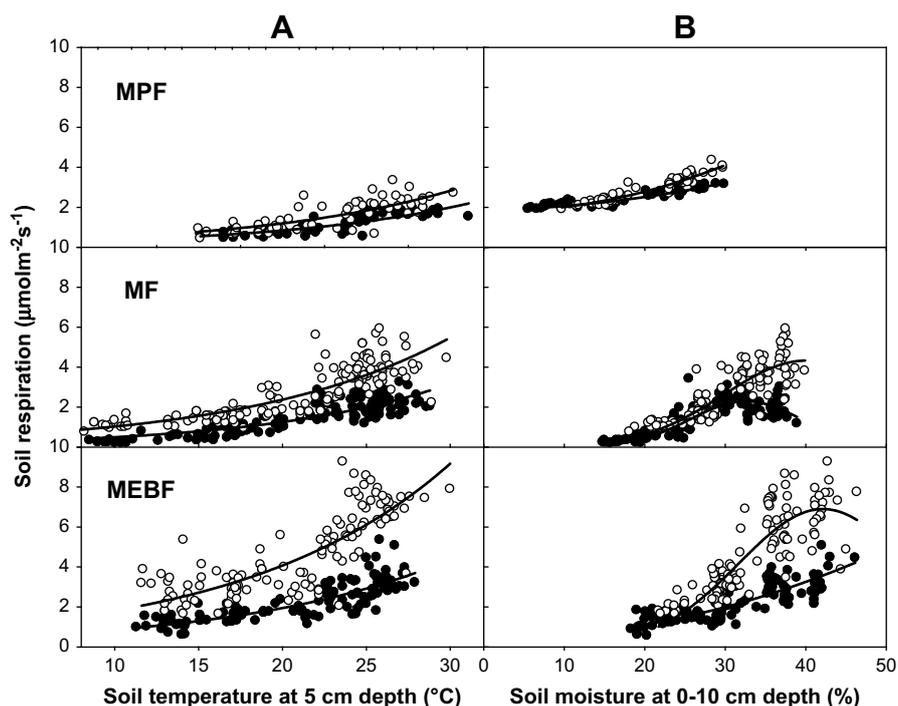


Fig. 5. Functions applied to the rate of soil respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) changes with soil temperature (A) at 5 cm depth ($^{\circ}\text{C}$) and soil moisture (B) at 0–10 cm depth (%) for three succession forest types. The symbols used are solid circles, the rate of soil respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) without litter cover and empty circles, the rate of soil respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) with litter cover. MPF, Masson pine forest; MF, mixed forest; MEBF, monsoon evergreen broad-leaved forest. A is function ($\text{SR} = a \exp(b\text{ST})$) and B is function ($\text{SR} = a_1 \exp(-0.5 (\text{SM} - c)^2/b_1^2)$), where ST and SM were soil temperature ($^{\circ}\text{C}$) at 5 cm depth and volumetric soil moisture (%) at 0–10 cm depth, respectively, SR is soil respiration ($\text{mmol m}^{-2} \text{s}^{-1}$), a , b , a_1 , b_1 and c are the regression coefficients.

and August, during the wet season (April to September), but diurnal variation in SR in MPF was still minimal. Although ST varied significantly through the day in all forest types and all seasons (Fig. 2), no significant differences between day-time and night-time SR were observed in our experiment. A likely explanation for this was that the chambers used were made of stainless steel and covered by the white cotton. They were not transparent. Therefore, the diurnal variation did not include photosynthetic uptake by forest floor vegetation during day-time. Moren and Lindroth (2000) pointed out that a peak of SR in a boreal forest may often occur near sunset. Similar results were found in earlier studies suggesting that SR exhibited a burst at dusk, which often was greater than the highest SR rates measured in the afternoon (Baldocchi et al., 1986). In our study, we observed this phenomenon only in some months and in some forest types. We were not convinced that this “dusk burst” was the normal pattern of diurnal variation. Baldocchi and Meyers (1991) suggested that their earlier measurements were not reliable, because of non-steady-state conditions caused by a rapid build-up of carbon concentration in the trunk space. To improve the understanding of the diurnal variation of SR at the forest floor, this process therefore must be studied further.

SR is highly correlated with ST and SM across seasons, but variation in SR rates in the diurnal observations was not directly related to ST and was also independent of SM. ST and SM have been

frequently identified as controlling factors of SR, but on a diurnal time scale, SM tends to be negatively correlated with ST so that their effects may tend to cancel each other and lead to relatively constant SR. Daily dynamics are therefore very different to monthly variation in SR, which is influenced by climate and is positively correlated with ST and SM variations. In the Dinghushan area, more than 80% of annual rainfall falls in the wet season (April to September), which coincides with high air temperature and active plant growth.

4.2. Spatial variation in SR with vegetation succession

SR in MEBF was usually the greatest and in MPF usually the least. This means the values of SR increased with the forest succession. To estimate the annual SR, we used the monthly SR rates for each forest stand to compute the sum for the year (Table 4). In the early succession stage, annual SR of the MPF ($592.1 \text{ g C m}^{-2} \text{ year}^{-1}$ with litter cover) stand was lower than those of adjacent later succession stages MF ($1023.7 \text{ g C m}^{-2} \text{ year}^{-1}$ with litter cover) and MEBF ($1163.0 \text{ g C m}^{-2} \text{ year}^{-1}$ with litter cover). This difference may be attributed to changes in the biological processes and their effect on environmental factors associated with natural forest succession.

The MPF pioneer community is almost monospecific, with only occasional broad-leaved tree species. The relatively low stand

Table 3
 a_1 , b_1 and c are the three regression coefficients in $\text{SR} = a_1 \exp(-0.5 (\text{SM} - c)^2/b_1^2)$ and r_1 is the correlation coefficient, where SM is volumetric soil moisture at 0–10 cm depth in % and SR is soil respiration in $\mu\text{mol m}^{-2} \text{s}^{-1}$. MPF, Masson pine forest; MF, mixed forest; MEBF, monsoon evergreen broad-leaf forest.

Forest type	Soil respiration without litter cover				Soil respiration with litter cover			
	a_1	b_1	c	r_1	a_1	b_1	c	r_1
MPF	21.8682	0.4194	1.2154	0.94	6.5396	0.2066	0.5555	0.95
MF	2.2912	0.0694	0.3257	0.85	4.3295	0.1026	0.4008	0.86
MEBF	10.1466	0.3376	0.9090	0.82	6.8991	0.1042	0.4212	0.86

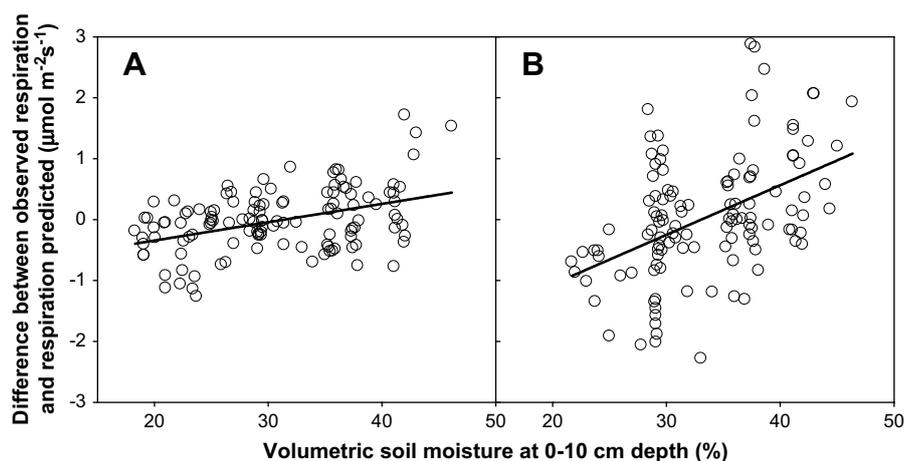


Fig. 6. Analysis of volumetric soil moisture (%) at 0–10 cm depth effects in terms of the residuals from the temperature function ($SR = a \exp(b ST)$, ST: soil temperature ($^{\circ}C$) at 5 cm depth; SR: soil respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$)) in monsoon evergreen broad-leaved forest. A is the plot without litter cover and B is the plot with litter cover.

density influences not only root biomass and soil microbial biomass, but also lower C inputs (roots, exudates and litter) to the soil (Table 5). With the succession to MF, heliophilous broad-leaved species invade the pioneer community and occupy the upper canopy, becoming the dominant species instead of *Pinus massoniana*. Root biomass and soil microbial biomass in this forest type were higher than in MPF (Yi et al., 2003). With the further development of a broad-leaved overstorey, root biomass and soil microbial biomass continued to increase and the shading of the forest stand led to higher relative humidity and higher rate of litter decomposition (Zhang et al., 2000). Litterfall and ground litter decomposition increased with the forest succession (Table 1), both influence soil C input. The microclimate and C inputs (root, exudates and litter) to the soil changed with the forest succession and resulted in higher CO_2 efflux rates in MEBF. Hence, MEBF, as a regional climax forest type in subtropical southern China, is adapted for relatively high SR conditions. Though MPF, MF, and MEBF stands are contiguous to each other, their apparent differences of SR might be caused by the heterogeneity of microhabitat. In agreement with our results, Raich and Schlesinger (1992) reported a positive effect of precipitation and air temperature on SR for all climate regions, however, the variation of SR rates within climate regions is very large. Interactions between biology and environment resulted in the maintenance of different patterns of SR for the Dinghushan forest types, which was related to the forest succession.

4.3. Factors controlling SR

SR is highly correlated with ST and SM across seasons. The functions ((1) and (2)) can explain 70–80% of the total variation in the measured mean SR over a period of 12 months for all six treatments. SR generally increases exponentially with ST and the relationship with SM is more complex. As SM increases, SR generally increases, but high SM can cause a decrease in SR rates. In the Dinghushan area, ST and SM covaried in different ways at different time scales: they had a positive relationship across seasons, but negative over 24 h. Caution is therefore required in deriving functions of respiration rates and relating them to ST and SM for the Dinghushan forest ecosystems. Some empirical models have been developed to describe the combination of ST and SM dependency of SR (Howard and Howard, 1993; Lloyd and Taylor, 1994; Savage and Davidson, 2001). These studies showed considerable scatter in the relations derived because ST and SM were not independent of each

other. Actually, the correlation parameter estimates in Table 2 based on an empirical function of temperature (1) apply to coupled ST and SM.

Q_{10} values have been used to describe ST dependence of SR. In this study, the Q_{10} values (Table 5) derived from function (1) appeared to decrease with the forest succession. The Q_{10} values in this paper included possible moisture limitations and therefore do not only represent a temperature but also a moisture dependency under field conditions. In the pioneer community MPF, microbial and root respiration showed a slightly stronger ST reaction compared with those in MF and MEBF (Yi et al., 2003), presumably because biological processes relating to the adaptation of SR to ST change became more effective with the forest succession. In fact, there were significant differences in microbial respiration for different forests or different seasons (Chen et al., 2004). This illustrated the interactions between biology and environment developing with the forest succession. So the response of SR rates to a future increase in ST may not be consistent at the different forest succession stages, as indicated by their different Q_{10} values.

The values of Q_{10} derived from function ($SR = k \exp^{\beta_1 ST} \exp^{\beta_2 SM}$) were 1.79, 2.01 and 2.28 for MEBF, MF and MPF, respectively. They were lower than those derived from the function (1) (Table 5). Our reported Q_{10} values were similar to the median value of 2.4 reported in a literature review of SR studies by Raich and Schlesinger (1992) and lower than Q_{10} values of 3.9 for the ambient plot and 5.7 for a drought plot in temperate forest soil described by Borken et al. (1999). Generally, Q_{10} values appear to be higher in cold regimes and lower under warm regimes. In cold regions, microbial and root respiration are more sensitive to temperature increase compared with a weak temperature reaction

Table 4

Annual forest floor respiration in a successional series of three subtropical forest types. Analyses of variance (ANOVA) were performed using soil respiration means to test the difference of soil respiration by forest at $\alpha = 0.05$ level. MPF, Masson pine forest; MF, mixed forest; MEBF, monsoon evergreen broad-leaf forest.

Forest type	MPF	MF	MEBF
Annual soil respiration without litter cover ($\text{g C m}^{-2} \text{year}^{-1}$)	426.5 \pm 35.8 ^a	561.7 \pm 41.1 ^b	850.8 \pm 88.2 ^c
Annual soil respiration with litter cover ($\text{g C m}^{-2} \text{year}^{-1}$)	592.1 \pm 58.2 ^a	1023.7 \pm 89.6 ^b	1163.0 \pm 120.5 ^{b, c}

Mean (SE) values within a row with different lowercase letters have significant forests differences at $\alpha = 0.05$ level.

Table 5
Relevant factors related to soil respiration in a successional series of three subtropical forest types. Analyses of variance (ANOVA) were performed using Q_{10} values to test the difference in Q_{10} between the types of forest at $\alpha = 0.05$ level. MPF, Masson pine forest; MF, mixed forest; MEBF, monsoon evergreen broad-leaf forest.

Forest type	Soil microbial biomass (mg C_{mic} 100 g ⁻¹ dry soil)	Root biomass (g m ⁻²)	Density of soil organic carbon (g m ⁻²)	Annual rate of litter decomposition (%)	Relative humidity (%)	Q_{10} of soil respiration without litter cover	Q_{10} of soil respiration with litter cover
MEBF	82.20	9600	16410	49.15	86.8	2.25 ^a	2.25 ^a
MF	58.62	8800	11129	40.84	81.8	2.36 ^b	2.31 ^b
MPF	52.99	8100	10518	36.90	80.5	2.37 ^{b, c}	2.37 ^c

Mean (SE) values within a column with different lowercase letters have significant forests differences at a 0.05 level. Data in table cited from Yi et al. (2003) and Zhang et al. (2000) except values of Q_{10} .

in temperate and tropical regions. The figures, 4.8 for Q_{10} value in boreal forest (Moren and Lindroth, 2000), 3.9 in temperate mixed hardwood forest (Davidson et al., 1998), 2.4 in subtropical forest in this study and often reported Q_{10} values less than 2.0 in the literature for tropical forests (Tjoelker et al., 2001), are in accord with this proposition.

Litterfall is a major pathway for SR through its decomposition processes. Those processes are determined not only by the amount of litter present but also by the components of the litter. Differences in SR between forest types were greater in plots with an intact litter layer, suggesting that litter respiration makes an important contribution to the increase in SR with the forest succession. Zhang et al. (2000) reported that the annual decomposition rates were 36.9, 40.8 and 49.2 for MPF, MF and MEBF, respectively. Litterfall and decomposition processes also strongly influence primary production and regulate energy flow and nutrient cycling in the forest ecosystems (Waring & Schlesinger, 1985). We found that litterfall increased with the forest succession (Table 1). Removal of surface litter significantly slowed down the decomposition of soil organic matter or root respiration or both. This study also found that removal of surface litter significantly increased the sensitivity of SR rate to ST. So, litter here is not only a source of CO₂ itself but also influences soil CO₂ efflux by indirect effects on biological processes in the underlying soil.

4.4. Conclusions

A static chamber is a forceful method to constrain estimation of SR change along with the forest succession as well as to identify important factors and controlling processes. In this study, we investigated the diurnal and seasonal variation of SR in the subtropical forests. The effects of ST and SM on SR were analyzed.

The annual SR in a climax forest community (MEBF) was 1163.0 g C m⁻² year⁻¹. In its succession communities, MF and MPF, the annual SR were 592.1 g C m⁻² year⁻¹, 1023.7 g C m⁻² year⁻¹, respectively. SR was usually the smallest in the early succession stage while showed the largest in the climax forest. This result suggested that the values of SR increased with the forest succession because of the changes in their species composition, soil biology, soil organic matter, and consequently their biogeochemical cycles.

Although ST varied significantly during day-time of all seasons in all forest types, no significant differences between day-time and night-time SR were observed in our experiment. A diurnal variation in SR was not directly related to ST. However, monthly dynamics of SR rates were strongly correlated with ST at 5 cm depth. In the study sites, ST and SM covaried in different ways at different time scales: they had a positive relationship across seasons, but negative over 24 h. Comparison of these different relationships could identify ST dependence of both seasonal and diurnal variation in SR.

The Q_{10} values appeared to decrease with the forest succession. In the early succession stage MPF, SR showed a stronger ST reaction compared with those in the later succession stages MF and MEBF.

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References

- Bakker, S.A., Jasperse, C., Verhoeven, J.T.A., 1997. Accumulation rates of organic matter associated with different successional stages from open water to carr forest in former turbaries. *Plant Ecology* 129, 113–120.
- Baldocchi, D.D., Meyers, T.P., 1991. Trace gas exchange above the floor of a deciduous forest 1. Evaporation and CO₂ efflux. *Journal of Geophysical Research* 96 (D4), 7271–7285.
- Baldocchi, D.D., Verma, S.B., Matt, D.R., Anderson, D.E., 1986. Eddy-correlation measurements of carbon dioxide efflux from the floor of a deciduous forest. *Journal of Applied Ecology* 23, 967–975.
- Banning, N.C., Grant, C.D., Jones, D.L., Murphy, D.V., 2008. Recovery of soil organic matter, organic matter turnover and nitrogen cycling in a post-mining forest rehabilitation chronosequence. *Soil Biology and Biochemistry* 40, 653–660.
- Black, C.C., 1973. Photosynthetic carbon fixation in relation to net CO₂ uptake. *Annual Review of Plant Physiology* 24, 253–286.
- Boone, R.D., Nadelhoffer, K.J., Canary, J.D., Kaye, J.P., 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature* 396, 570–572.
- Borken, W., Xu, Y.-J., Brumme, R., Lamersdorf, N., 1999. A climate change scenario for carbon dioxide and dissolved organic carbon fluxes from a temperate forest soil: drought and rewetting effects. *Soil Science Society of America Journal* 63, 1848–1855.
- Borken, W., Yijun, X., Davidson, E.A., Beese, F., 2002. Site and temporal variation of SOIL RESPIRATION in European beech, Norway spruce, and Scots pine forests. *Global Change Biology* 8, 1205–1216.
- Chen, G.S., Yang, Y.S., Xie, J.S., Li, L., Gao, R., 2004. Soil biological changes for a natural forest and two plantations in subtropical China. *Pedosphere* 14 (3), 297–304.
- Cote, L., Brown, S., Pare, D., Fyles, J., Bauhus, J., 2000. Dynamics of carbon and nitrogen mineralization in relation to stand type, stand age and soil texture in the boreal mixedwood. *Soil Biology and Biochemistry* 32, 1079–1090.
- Davidson, E.A., Belk, E., Boone, R.D., 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biology* 4, 217–227.
- Davidson, E.A., Janssens, I.A., Luo, Y.Q., 2006. On the variability of respiration in terrestrial ecosystems: moving beyond Q_{10} . *Global Change Biology* 12, 154–164.
- De Kovel, C.G.F., Van Mierlo, A.J.E.M., Wilms, Y.J.O., Berendse, F., 2000. Carbon and nitrogen in soil and vegetation at sites differing in successional age. *Plant Ecology* 149, 43–50.
- Dobson, A.P., Bradshaw, A.D., Baker, A.J., 1997. Hopes for the future: restoration ecology and conservation biology. *Science* 277, 515–522.
- Drewitt, G.B., Black, T.A., Nescic, Z., Humphreys, E.R., Jork, E.M., Swanson, R., Ethier, G.J., Griffis, T., Morgenstern, K., 2002. Measuring forest floor CO₂ fluxes in a Douglas-fir forest. *Agricultural and Forest Meteorology* 110, 299–317.
- Goodale, C.L., Apps, M.J., Birdsey, R.A., Field, C.B., Heath, L.S., Houghton, R.A., Jenkins, J.C., Kohlmayer, G.H., Kurz, W., Liu, S.R., Nabuurs, G.J., Nilsson, S., Shvidenko, A.Z., 2002. Forest carbon sinks in the Northern Hemisphere. *Ecological Applications* 12, 891–899.
- Grace, J., 2004. Understanding and managing the global carbon cycle. *Journal of Ecology* 92 (2), 189–202.
- Hanson, P.J., Wullschlegel, S.D., Bohlmann, S.A., Todd, D.E., 1993. Seasonal and topographic patterns of forest floor CO₂ efflux from an upland oak forest. *Tree Physiology* 13, 1–15.
- Howard, D.M., Howard, P.J.A., 1993. Relationship between CO₂ evolution, moisture content and temperature for a range of soil types. *Soil Biology and Biochemistry* 25, 1537–1546.
- Irvine, J., Law, B.E., 2002. Contrasting soil respiration in young and old-growth ponderosa pine forests. *Global Change Biology* 8, 1183–1194.

- Jenkinson, D.S., Adams, D.E., Wild, A., 1991. Model estimates of CO₂ emission from soil in response to global warming. *Nature* 351, 304–306.
- Jia, B.R., Zhou, G.S., Wang, F.Y., Wang, Y.H., Yuan, W.P., Zhou, L., 2006. Partitioning root and microbial contributions to soil respiration in *Leymus chinensis* populations. *Soil Biology and Biochemistry* 38, 653–660.
- Jia, G.M., Cao, J., Wang, C.Y., Wang, G., 2005. Microbial biomass and nutrients in soil at the different stages of secondary forest succession in Ziulin, northwest China. *Forest Ecology and Management* 217, 117–125.
- Kong, G.H., Huang, Z.L., Zhang, Q.M., Liu, S.Z., Mo, J.M., He, D.Q., 1997. Type, structure, dynamics and management of the lower subtropical evergreen broad-leaved forest in the Dinghushan Biosphere Reserve of China. *Tropics* 6 (4), 335–350.
- Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. *Functional Ecology* 8, 315–323.
- Moren, A.-S., Lindroth, A., 2000. CO₂ exchange at the floor of a boreal forest. *Agricultural and Forest Meteorology* 101, 1–14.
- Peng, S.L., Wang, B.S., 1995. Forest succession at Dinghushan, Guangdong, China. *Chinese Journal of Botany* 7 (1), 75–80.
- Peterjohn, W.T., Melillo, J.M., Steudler, P.A., Newkirk, K.M., Bowles, F.P., Aber, J.D., 1994. Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. *Journal of Applied Ecology* 4, 617–625.
- Raich, J.W., Schlesinger, W.H., 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44B, 81–99.
- Raich, J.W., Tufekcioglu, A., 2000. Vegetation and soil respiration: correlations and controls. *Biogeochemistry* 48, 71–90.
- Savage, K., Davidson, E.A., 2001. Interannual variation of soil respiration in two New England forests. *Global Biogeochemical Cycles* 15, 337–350.
- Schlentner, R.E., Van Cleve, K., 1985. Relationships between CO₂ evolution from soil, substrate temperature and substrate moisture in four mature forest types in interior Alaska. *Canadian Journal of Forest Research* 15, 97–106.
- Schlesinger, W.H., Andrews, J.A., 2000. Soil respiration and the global carbon cycle. *Biogeochemistry* 48, 7–20.
- Sheil, D., 2001. Long-term observations of rain forest succession, tree diversity and responses to disturbance. *Plant Ecology* 155, 183–199.
- Thuille, A., Buchmann, N., Schulze, E.D., 2002. Carbon stocks and soil respiration rates during deforestation, grassland use and subsequent Norway spruce afforestation in the Southern Alps, Italy. *Tree Physiology* 20, 849–857.
- Tjoelker, M.G., Oleksyn, J., Reich, P.B., 2001. Modelling respiration of vegetation: evidence for a general temperature-dependent Q₁₀. *Global Change Biology* 7, 223–230.
- Tolosa, F.J.X., Vester, H.F.M., Marcial, N.R., Albores, J.C., Lawrence, D., 2003. Leaf litter decomposition of tree species in three successional phase of tropical dry secondary forest in Campeche, Mexico. *Forest Ecology and Management* 174, 401–412.
- Waring, R.H., Schlesinger, W.H., 1985. *Forest Ecosystems: Concepts and Management*. Academic Press, Orlando, FL, pp. 181–120.
- Woo, M.K., Fang, G.X., DiCenzo, P.D., 1997. The role of vegetation in the retardation of soil erosion. *Catena* 29 (2), 145–159.
- Yan, J.H., Zhou, G.Y., Zhang, D.Q., Chu, G.W., 2007. Changes of soil water, organic matter, and exchangeable cations along a forest successional gradient in Southern China. *Pedosphere* 17 (3), 397–405.
- Yi, Z.G., Yi, W.M., Zhou, G.Y., Ding, M.M., Zhou, L.X., 2003. Soil carbon effluxes of three major vegetation types in Dinghushan Biosphere Reserve. *Acta Ecologica Sinica* 23, 1673–1678.
- Zhang, D.Q., Ye, W.H., Yu, Q.F., Kong, G.H., Zhang, Y.C., 2000. The litter-fall of representative forests of successional series in Dinghushan. *Acta Ecologica Sinica* 20 (6), 938–944.
- Zhou, G.Y., Liu, S.G., Li, Z.A., Zhang, D.Q., Tang, X.L., Zhou, C.Y., Yan, J.H., Mo, J.M., 2006. Old-growth forests can accumulate carbon in soils. *Science* 314, 1417.
- Zhou, G.Y., Yan, J.H., 2000. *Theories and Practice of Compensation for Ecological Forests*. China Meteorological Press, Beijing, pp. 17–25.
- Zhou, G.Y., Yan, J.H., 2001. The influences of regional atmospheric precipitation characteristics and its element inputs on the existence and development of Dinghushan forest ecosystems. *Acta Ecologica Sinica* 21, 2002–2012.