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Partitioning soil respiration of subtropical forests with different successional stages in south China

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Abstract

The methods of root-excision and trenching were employed concurrently in the present study in order to partition total soil respiration (R_{total}) into root respiration (R_{root}), rhizomicrobial respiration (R_{rhizo}) and root free soil microbial respiration (R_{rfs}). This study was conducted under the monsoon evergreen broad-leaf forest (BF), the pine forest (PF) and the pine and broad-leaf mixed forest (MF) in Dinghushan Biosphere Reserve, subtropical China from April 2001 to March 2002. The three forests represent different successional stages in this region. Our results showed that mean R_{total} were 477.9 \pm 96.3, 429.5 \pm 61.0 and 435.4 \pm 95.1 mg CO₂ m⁻² h⁻¹ in BF, PF and MF, respectively. R_{total} were significantly higher in rain season than those in dry season. However, no significant variations were found among three forests. Soil respiration rates were highly dependent on the combined effects of soil temperature and soil water content. R_{root} was significantly higher in rain season than that in dry season, with the values of 113.8–166.0 mg CO₂ m⁻² h⁻¹ in rain season and 48.6–97.1 mg CO₂ m⁻² h⁻¹ in dry season. There were no significant differences for R_{rfs} and R_{rhizo} between rain and dry season. However, the contributions of each component to R_{total} in rain season differed from those in dry season, R_{root} -to- R_{total} , R_{rfs} -to- R_{total} and R_{rhizo} -to- R_{total} and R_{rhizo} -to- R_{total} and R_{rhizo} -to- R_{total} and R_{rhizo} between 18.1–22.1, 44.8–47.6 and 30.3–37.1%, respectively.

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1. Introduction

In recent years, much attention has been paid on soil respiration because it is recognized as a major soil carbon efflux and one of the key components of the carbon cycle in terrestrial ecosystems (Raich and Schlesinger, 1992; Raich and Potter, 1995). It was reported that soil respiration could represent 40–90% of the forest ecosystem respiration (Schlesinger and Andrews, 2000). On a global scale, soil respiration produces 80.4 Pg CO₂-C annually, which is approximately 10-fold greater than that from fossil fuel combustion and deforestation sources combined (Raich et al., 2002), and thus even small changes in soil respiration may greatly influence atmospheric carbon and heat balance (Veenendaal et al., 2004; Kane et al., 2005). Recently, soil respiration has become a central issue in

global change ecology because of its controversial role in global warming process (Giardina and Ryan, 2000).

Previous interpretation of soil CO_2 fluxes emphasized particularly on the measurement of R_{total} , which was usually separated into two components: root respiration and microbial respiration. However, rhizomicrobial respiration was not distinguished from root-free soil microbial respiration (Raich and Nadelhoffer, 1989). Rhizomicrobial respiration used to be considered as a component of either root respiration or microbial respiration depending upon researchers' preference. Actually three biologically relevant compartments were involved in soils and they were defined as root tissue, rhizosphere soil and root-free soil, and thus soil respiration could be separated into three components, which could be defined as R_{root} , R_{rhizo} and R_{rfs} .

Partitioning R_{total} into three components and defining the variables controlling each component is difficult but important, and it can help us better understand the belowground carbon dynamics (Kelting et al., 1998; Ohashi et al., 2000). For

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instance, calculating C loss through root respiration could help us estimate gross primary production more accurately, and estimating C loss through heterotrophic microbial respiration must be known in order to calculate net ecosystem production (Kuzyakov and Larionova, 2005). On the other hand, the SOMderived CO₂ is mainly from the microbial decomposition of soil organic matter (SOM), therefore, the calculation of microbial respiration can help us to estimate the amount of carbon ultimately stored in soil (Sulzman et al., 2005). Furthermore, separate estimation of R_{root} , R_{rhizo} and R_{rfs} is also a prerequisite for modeling CO₂ fluxes from soil (Lee et al., 2003). Thus, the contribution of each component to soil respiration must be known in order to understand the effect of climate change, forest age and forest succession on C cycling (Melillo et al., 2002; Bond-Lamberty et al., 2004).

No studies on partitioning R_{total} have been performed in subtropical forests in China. The forested area in south China is about one-third of the total forested area of China, therefore, research on C flux in this area is very important to calculate the forest C budget of China. Thus, the objectives of this study were: (i) to separate R_{total} into R_{root} , R_{rhizo} and R_{rfs} , and (ii) determine the contribution of the three components to R_{total} in three forests in subtropical China. For this purpose, the methods of root-excision and trenching were employed concurrently. The root excision method enables us to separate R_{root} from microbial respiration (including R_{rhizo} and R_{rfs}), and the trenching method enables us to separate R_{rfs} from rhizosphere respiration (including R_{root} and R_{rhizo}); consequently, the three components: R_{root} , R_{rhizo} and R_{rfs} can be partitioned.

2. Materials and methods

2.1. Site description

The entire study took place from April of 2001 to March of 2002 in Dinghushan Biosphere Reserve (DBR, 23°09'21" to 23°11'30"N, and 112°30'39" to 112°33'41"E), China. DBR is at the southern subtropical edge of south China and lies on the southeast part of Eurasia. It is near the Pacific Ocean to the east and the Indian Ocean to the South and has a southern subtropical monsoon climate. The mean annual temperature is 21 °C and the mean annual rainfall is 1927 mm. April through September represents the rain season with the mean monthly rainfall of 200 mm. November to January represents the dry season with the mean monthly rainfall from 22 to 50 mm. The soil in this area consists mainly of lateritic red-earth and yellow-earth. Monsoon evergreen broad-leaf forest (BF), pine forest (PF), pine and broad-leaf mixed forest (MF) were selected in the present study. The age of BF is about 400 years, with average stem diameter above 20 cm, canopy height above 20 m. The component species of the main community is Castanopsis chinensis, Schima superba, Cryptocarya spp. There were 3531 stems per hectare in BF in 1999. The age of MF is about 60 years, with average stem diameter of 12-20 cm, canopy height of 8-14 m. The component species of the main community is Pinus massoniana, Schima superba, Castanopsis chinensis. There were 3890 stems per hectare in MF in 1999. The age of PF is about 60 years, with

Forest type [#]	Bulk density	Mean annual soil (10 cm depth) temperature (°C)	pН	Organic carbon (g kg ⁻¹)	NH_4-N (mg kg ⁻¹)
BF	0.85	19.6	3.76	3.89	23.4
MF	1.03	20.5	3.80	2.68	23.7
PF	1.40	21.9	4.04	2.33	28.9

[§] Soils of 0–15 cm depth except for soil temperature.

[#] BF, MF and PF refer to Monsoon evergreen broad-leaved forest, Pine and Broad-leaved mixed forest, and Pine forest, respectively.

average stem diameter of 25 cm, canopy height of 8–12 m. The component species of the main community is *Pinus massoniana–Rhodomyrtus tomentosa–Dicranopteris linearis* var. dichotoma (He et al., 1982; Wang et al., 1982; Ding et al., 2001). Some soil properties of experimental sites are presented in Table 1.

2.2. Soil CO_2 flux

Soil CO₂ flux was measured once at the end of each month from April to September 2001 (rain season) and from October 2001 to March 2002 (dry season) with a portable infrared gas analyzer (Li-6250, LI-COR Inc., Lincoln, NE) attached to a dynamic soil respiration chamber of 7.1 cm in diameter and 8.1 cm in height. The chamber was gently inserted into the forest floor to a depth of 2 cm. Ambient air at 2 m above soil surface was drawn into the chamber and air inside the chamber was well mixed with a small electronic fan. The air was then drawn out of the chamber through an outlet with plastic tubing connected to the IRGA for analysis (Fig. 1). Respiration rates were calculated using Eq. (1):

$$R = K_{\rm CO_2} \left(\frac{273}{T}\right) \left(\frac{P}{101.3}\right) (C_{\rm out} - C_{\rm in}) \frac{F}{A} \tag{1}$$



Fig. 1. The description of the dynamical chamber for soil respiration measurement.

where *R* is the respiration rate (mg CO₂ m⁻² h⁻¹), K_{CO_2} (1.9643 × 10⁻³ mg CO₂ µl⁻¹) unit conversion factor for calculating CO₂ flux rate, *T* air temperature (K), *P* atmospheric pressure (kPa), C_{out} and C_{in} are the CO₂ concentration of the outlet and inlet of the chamber (µl l⁻¹), respectively, *F* flow rate of the air (l h⁻¹), and *A* the area of the soil covered by the chamber (m²).

Nine replicate plots of $0.5 \text{ m} \times 0.5 \text{ m}$ with the distance of 4–5 m were established in each forest. One measurement was made per plot during each sampling. Soil temperature was measured with thermocouples (TES Electrical Electronic Corp., Taipei, Taiwan), and soil water content was measured with moisture probe meter (MPM-160, ICT international). Nine different sites were selected for soil temperature and soil water measurement at the time of sampling.

2.3. Partitioning soil CO_2 flux

The components of R_{total} were determined using a modified trenching technique combined with root excision method. Roots were sorted out from soil, washed and blotted dry. The live roots were separated from the dead roots on the basis of color, brittleness, structure of cortex or bark, and color of xylem. Root respiration was then measured with an IRGA attached to a dynamic root chamber constructed of stainless steel cylinders, 10.5 cm in diameter and 10.5 cm in height. Respiration rate was calculated using Eq. (2):

$$R = K_{\rm CO_2} \left(\frac{273}{T}\right) \left(\frac{P}{101.3}\right) (C_{\rm out} - C_{\rm in}) F \frac{B}{W}$$
(2)

where *W* is the root weight in soil core (g), and *B* root biomass (g m⁻²). The other parameters are the same as Eq. (1). All root respiration measurements were made within 30 min after root excision. Field measurements of root respiration were performed at the end of April and October. Microbial respiration (R_{micro}), including R_{rhizo} and R_{rfs} , could then be calculated by subtracting R_{root} from R_{total} (see Eq. (3)).

In order to separate $R_{\rm rhizo}$ from $R_{\rm rfs}$, the trenching technique was employed. Namely, nine plots of $0.5 \text{ m} \times 0.5 \text{ m}$ with the distance of 4-5 m were established and a trench of 0.2 m wide and 1 m deep around the plot were dug. After lining the trench with polyethylene nets of 0.08 mm mesh size, soil were refilled back into the trench according to its original soil profiles. The trenching cut down the live roots extended into the plots and did not influence soil water content. The plots were then kept free of seedlings and herbaceous vegetation by periodic manual removal. These nine plots were established about 2 m away from the control plots. R_{total} was measured in both trenched and un-trenched control plots. Since the temperature varied between the months, soil respiration rates of trenchedplots were normalized using Q_{10} values of the same forests obtained in the present study. Due to the lack of fresh C input from plants and the freshly severed root material decomposition, total soil respiration decreased and eventually reached a horizontal asymptote (Fig. 2). The respiration rate at this asymptote phase represented $R_{\rm rfs}$. $R_{\rm rhizo}$ was estimated by



Fig. 2. Change of soil respiration after plots have been trenched in rain season (a) and in dry season (b). BF (solid circles), MF (open circles) and PF (triangles). The values were the averages of nine measurements per site, and the bars were the standard deviations.

subtracting R_{rfs} from R_{micro} (see Eq. (4)) (Kelting et al., 1998; Kuzyakov and Larionova, 2005; Tang et al., 2005; Chen et al., 2006).

$$R_{\rm micro} = R_{\rm total} - R_{\rm root} \tag{3}$$

$$R_{\rm rhizo} = R_{\rm micro} - R_{\rm rfs} \tag{4}$$

Considering both the time and the CO₂ concentration might affect the root respiration after root excision, we conducted two separate experiments to correct these potential effects. In the first experiment, the seedlings of Cryptocarya concinna and Pinus massoniana were selected to measure the root respiration before and after the roots had been excised. Three seedlings of each species were extracted and the roots were cleaned to get rid of attached soil particles to eliminate rhizosphere microbial respiration. Root respiration was measured with an IRGA (Li-6200, LI-COR Inc., Lincoln, NE) attached with a root chamber, which was constructed of stainless steel cylinders (10.5 cm in diameter and 10.5 cm in height). Root respiration rates before excision were recorded as the initial root respiration (R_0) . Then the roots were excised from the plants and kept in the root chamber under constant humidity and temperature, root respiration rates were

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measured at 5, 15, 30, 60, 90, 120, 150, 190, 250, 310, 380, 460, 610 min after roots excision and the rate of 30 min after excision was represented as R_{30} . The ratio of R_{30} to R_0 was then obtained and used for correcting the respiration of excised roots. In the second experiment, the respiration of 2500 ppm ($R_{root-2500}$) and 400 ppm ($R_{root-400}$). The reason for this experiment was that the mean CO₂ concentrations were 2519 \pm 1927 ppm at the soil depth of 45 cm but only 433 \pm 12 ppm for ambient air, and it was reported that CO₂ concentration around roots could affect root respiration significantly (Burton et al., 1997; Lipp and Andersen, 2003). The ratio of $R_{root-2500}$ to $R_{root-400}$ was then obtained and used for correcting the root respiration.

2.4. Root biomass and soil microbial biomass

Root biomass at each forest was estimated by taking soil cores. Nine soil cores of 40 cm (length) \times 25 cm (width) \times 60 cm (depth) were taken in each forest at the end of April and October in 2001.The roots were picked out, cleaned with water, oven-dried at 80 °C and weighed.

Nine soil samples of 0–15 cm soil layer beside the control plots were taken in April and October 2001. Soil microbial biomass was measured using fumigation-incubation (FI) method (Jenkinson and Powlson, 1976).

2.5. Data analysis

A one-way ANOVA was used to compare R_{total} , R_{root} , R_{rhizo} and R_{micro} between the three forests and Fisher's least significant difference (LSD) procedure was used for multiple comparison analysis. T-test was conducted to compare the difference between the dry and rain season. Non-linear regression analysis was used to examine the correlation of the soil respiration rate with the temperature and soil water content. Statistical calculations were performed using SPSS 10.0 for Windows and SigmaPlot 9.0.



Fig. 3. Change of root respiration rate after roots have been excised. Bars refer to standard deviations (N = 3).

3. Results

3.1. Root respiration rates after excision and under different CO_2 concentration

Root respiration rates decreased quickly after the roots were excised from the plants. The ratio of R_{30} to R_0 was about 0.52 ± 0.05 for both species (Fig. 3). The respiration rates of the excised roots were significantly lower under the CO₂ concentration of 2500 ppm ($R_{\text{root-2500}}$) than those under 400 ppm ($R_{\text{root-400}}$). The ratio of $R_{\text{root-2500}}$ to $R_{\text{root-400}}$ was 0.33 ± 0.20 (N = 17).



Fig. 4. Soil temperature (a), soil moisture (b) and soil respiration (c) under three forests. BF (solid circles), MF (open circles) and PF (triangles). Bars refer to standard deviations (N = 9).



Fig. 5. Root biomass (a) and soil microbial biomass (b) under BF, MF and PF. Bars refer to standard deviations (N = 9). # means significant difference of root biomass between rain season and dry season in all three forests. * means significantly higher soil microbial biomass in BF than those in MF and PF in rain season and dry season.

3.2. Soil temperature and soil water content

Soil temperature at 10 cm depth did not differ across three forests. The mean soil temperatures ranged from 13.6 to $25.0 \,^{\circ}$ C, 15.8 to 27.3 $^{\circ}$ C and 14.4 to 27.2 $^{\circ}$ C at soil depth of 10 cm in BF, PF and MF, respectively (Fig. 4a). The maximum values were recorded in July or August and the minimum in January or February.

Soil water content did not show significant seasonal fluctuation, and it ranged from 20.2 to 28.8%, 10.9 to 19.2% and 11.4 to 22.0% in BF, PF and MF, respectively (Fig. 4b). The maximum soil water content was recorded in May or June and the minimum in January. Soil water content in BF was significantly higher than those in MF and PF (p < 0.05), but it was not significantly different between MF and PF.

3.3. Root biomass and soil microbial biomass

The mean root biomass was 11.1 ± 4.4 , 9.3 ± 1.9 and 10.3 ± 3.5 t ha⁻¹ in rain season and 8.3 ± 4.7 , 7.4 ± 4.3 and 8.2 ± 2.0 t ha⁻¹ in dry season in BF, PF and MF, respectively. No significant variance of the root biomass was found between three forests, but the root biomass differed significantly between rain season and dry season in all three forests (p < 0.05) (Fig. 5a).

The mean soil microbial biomass was 687 ± 113 , 520 ± 45 , $534 \pm 43 \ \mu g \ C_{mic} \ g^{-1}$ dry soil in rain season and 617 ± 37 , 446 ± 62 , $474 \pm 77 \ \mu g \ C_{mic} \ g^{-1}$ dry soil in dry season in BF, PF and MF, respectively. The microbial biomass was significantly higher in BF than those in MF and PF (p < 0.05), but no significant difference was found between MF and PF. Soil microbial biomass did not differ significantly between the rain season and the dry season (Fig. 5b).



Fig. 6. Total soil respiration (a), root respiration (b), root-free soil respiration (c) and rhizomicrobial respiration (d) under three forests. Bars refer to standard deviations (N = 9).

3.4. Rates of R_{total}, R_{root}, R_{rfs} and R_{rhizo}

 R_{total} ranged from 344.5 to 684.9 mg CO₂ m⁻² h⁻¹ in BF, 328.0 to 547.2 mg CO₂ m⁻² h⁻¹ in PF, and 290.1 to 635.4 mg CO₂ m⁻² h⁻¹ in MF, with the average of 477.9 ± 96.3, 429.5 ± 61.0 and 435.4 ± 95.1 mg CO₂ m⁻² h⁻¹ in BF, PF and MF, respectively. It did not differ significantly between the forests. R_{total} increased in summer and decreased in winter, which corresponded to the seasonal change of soil temperature (Fig. 4a, c). R_{total} was significantly higher in rain season than that in dry season (p < 0.05) (Fig. 6a).

The mean rates of R_{root} were 131.5 ± 53.6, 96.2 ± 33.6 and 105.8 ± 44.3 mg CO₂ m⁻² h⁻¹ in BF, PF and MF, respectively. R_{root} tended to be higher in BF than that in MF and PF, and it tended to be higher in rain season than that in dry season under all the forests (Fig. 6b).

 $R_{\rm rfs}$ obtained at the "asymptote" phase by trenching method were 204.8 ± 57.8, 162.8 ± 50.7 and 177.3 ± 61.3 mg CO₂ m⁻² h⁻¹ in rain season and 208.9 ± 41.5, 194.3 ± 34.8 and 195.7 ± 46.4 mg CO₂ m⁻² h⁻¹ in dry season in BF, PF and MF, respectively. Significant difference of $R_{\rm rfs}$ was not observed among the three forests, nor between the rain season and the dry season (Fig. 6c).

The estimated $R_{\rm rhizo}$ were 97.9 ± 25.1, 159.6 ± 47.3 and 132.3 ± 27.0 mg CO₂ m⁻² h⁻¹ in the rain season and 132.6 ± 21.5, 160.9 ± 50.2 and 141.3 ± 37.5 mg CO₂ m⁻² h⁻¹ in the dry season in BF, PF and MF, respectively. $R_{\rm rhizo}$ tended to be higher in the rain season than that in the dry season, but it did not differ significantly (Fig. 6d).

3.5. The ratios of R_{root} , R_{rfs} and R_{rhizo} to R_{total}

The contributions of different components to R_{total} differed between the forests in both the rain and the dry season. In the rain season, R_{root} -to- R_{total} and R_{rfs} -to- R_{total} ratios in BF were higher than those in MF and PF. Significant differences of R_{rhizo} -to- R_{total} ratios were found between the forests, with the highest values in PF and the lowest in BF. In the dry season, there were no significant differences of R_{root} to- R_{total} and R_{rfs} -to- R_{total} ratios between the forests, but significant difference of R_{rhizo} -to- R_{total} ratios were found between the forests. The R_{root} -to- R_{total} ratios in the rain season were significantly higher than those in the dry season (Table 2).

4. Discussion

4.1. Contributions of soil respiration components to R_{total}

Contributions of R_{root} , R_{rhizo} and R_{rfs} to R_{total} varied with soil types, vegetation types, forest age, environmental conditions and methods employed (Kelting et al., 1998; Andrews et al., 1999; Hanson et al., 2000; Chen et al., 2006). Hanson et al. (2000) summarized about 50 reports and found that the contribution of the R_{root} to R_{total} ranged from 30 to 80%, with the mean ratios of 48% from autotrophic respiration for forest and 60% for nonforest ecosystems. Through the meta-analysis of the soil respiration partitioning studies from the literature of the past 30 years, Subke et al. (2006) found that the contribution of heterotrophic respiration to total soil respiration decreased with the increase of annual soil respiration for forest ecosystems. Kelting et al. (1998) estimated that $R_{\rm root}$, $R_{\rm rhizo}$ and $R_{\rm rfs}$ contributed 32, 20 and 48% to $R_{\rm total}$ in forest, respectively. Chen et al. (2006) found that R_{root} , R_{rhizo} and R_{rfs} accounted for 43-66, 29-53 and 1-5% under radiata pine, respectively.

In the present study, the R_{root} -to- R_{total} ratios ranged from 18.1 to 35.4%, with higher values in the rain season and lower values in the dry season. The different ratios between the rain and dry season could be attributed to the different reaction of autotrophic and heterotrophic respiration to soil water content (Andersen et al., 2005). On the other hand, the higher R_{root} -to- R_{total} ratios in rain season could be owed to the phenology in DBR. Here there was an obvious seasonal wet-dry cycle accompanied by a biotic growth cycle. The plants started germinating from March to May, flowering from March to June, and fruiting from July to October (Li and Wang, 1984). The plants grew faster and higher root biomasses were recorded in the rain season (Fig. 5a), which resulted in higher root respiration. Only the R_{root} -to- R_{total} ratios in rain season in the present study were comparable to those obtained from other forest ecosystems (Bowden et al., 1993; Kelting et al., 1998). The ratios were higher than 23% reported by Sulzman et al. (2005), who obtained the rhizospheric respiration (including root and rhizomicrobial respiration) by the difference of control and trenched plots for forest ecosystem. The ratios were lower than that obtained by other studies using trenching method in forests (Ewel and Cropper, 1987; Tang et al., 2005). Rroot in their study actually included both root respiration and rhizomicrobial respiration. The ratios in our study would be

Table 2					
Contribution	of different	components	to total	soil respira	tion

Component	Rain season	Rain season			Dry season		
	BF	MF	PF	BF	MF	PF	
$R_{\rm root}$ (%)	35.4(8.5)	29.1(6.3)	26.1(5.6)	22.1(4.4)	20.0(4.6)	18.1(5.4)	
$R_{\rm rfs}$ (%)	43.7(6.7)	40.6(9.1)	37.3(10.1)	47.6(10.2)	46.4(8.1)	44.8(10.5)	
$R_{\rm rhizo}$ (%)	20.9(5.4)	30.3(7.5)	36.6(8.0)	30.2(7.4)	33.5(7.3)	37.1(9.7)	

Data are means, standard deviations in parentheses, N = 9.

Table 3		
Correlation equations between	soil respiration and soil temperature and soil water content	

Forest type	Equation	R^2
BF MF PF	$\begin{split} R &= -2812.8 - 98.4(T_{10}) + 2.8(T_{10} \times T_{10}) + 372.2(W) - 6.5(W \times W) \\ R &= -249.4 - 97.9(T_{10}) + 2.4(T_{10} \times T_{10}) + 182.5(W) - 5.0(W \times W) \\ R &= 314.6 - 84.2(T_{10}) + 2.0(T_{10} \times T_{10}) + 119.7(W) - 3.6(W \times W) \end{split}$	$\begin{array}{c} 0.81^{*} \\ 0.91^{**} \\ 0.87^{**} \end{array}$

Soil respiration (mg CO₂ m⁻² h⁻¹), soil temperature at 10 cm deep soil (°C) and soil water content (% m/m) are represented as R, T_{10} and W, respectively. Significant at a 0.05 level.

Significant at a 0.01 level.

comparable to those results if the $R_{\rm rhizo}$ had been included in R_{root} in the present study. Using trenching methods, Bond-Lamberty et al. (2004) found that minimal annual root respiration was 5% of total respiration in the recently burned stands, 40% in the 21-year-old stands and 5-15% in the oldest (152-year-old) stands. The R_{root} -to- R_{total} ratios in DBR were also lower than those obtained by other study (Ohashi et al., 2000). This was probably attributable to the low contribution of the root biomass in DBR. In general, the ratio of the root to the total plant biomass was about 25-30% (Vogt et al., 1996), but it was only about 18.8% in DBR (Zhang and Ding, 1996).

Table 2 showed that the annual mean ratios of R_{rfs} -to- R_{total} were 45.7, 41.1 and 43.5% in BF, PF and MF, respectively. Our values were within the range of the ratios reported in the northeast China using the same trenching method (Jiang et al., 2005). Our values were also comparable to those estimated with three-compartment model by Kelting et al. (1998), but were much lower than those estimated with two-compartment model (Bowden et al., 1993). $R_{\rm rhizo}$ was considered to be part of the $R_{\rm rfs}$ in the two-compartment model of Bowden et al. (1993), which caused a higher value of the $R_{\rm rfs}$.

4.2. Factors controlling soil respiration

It was reported that soil respiration was controlled by a range of biotic and abiotic factors, such as temperature, soil water content, aboveground vegetation structure, photosynthetic activity, or plant phenological development (Subke et al., 2006). Soil respiration rates have been found to increase linearly, sinusoidally or logarithmically with soil temperature (Raich and Schlesinger, 1992). The correlations between the soil respiration and the temperature were also found in the present study. The Q_{10} values were 1.26–1.46, which were lower than those reported for temperate forests (Raich and Schlesinger, 1992; Bowden et al., 1998). We considered that the seasonal variation of the soil temperature was smaller in the tropical and subtropical forests than that in temperate forests; therefore, soil respiration was not so sensitive to soil temperature as that in temperate forests.

The correlations between soil respiration and soil water were significant (p < 0.05). Soil water content of 15–25% was detected to be optimal for soil respiration. However, Sulzman et al. (2005) found the relationship between soil respiration and soil water was poor and they concluded that it was because that the optimal water content is bimodal and out of phase with biologically optimal temperature.

Considering both soil water content (W) and soil temperature (T) as the major variables affecting soil respiration, multiple regressions were established (Table 3). The values of R^2 were improved compared to those considering the soil temperature or the soil water content alone, suggesting soil respiration was influenced concurrently by these two factors. The similar correlation between the soil respiration and the temperature and soil water content were also found by other studies (Bowden et al., 1998; Fernandez et al., 1993).

Other factors besides the temperature and soil water also influenced soil respiration. As mentioned above, higher root biomass in rain season caused higher root respiration and soil respiration in rain season. Same to the root biomass, the soil microbial biomass in rain season was higher than that in dry season (Fig. 5b), which suggested that soil microorganisms influenced soil respiration. Adachi et al. (2006) also found that soil respiration increased with fine root biomass and microbial biomass in the tropical forests. These results suggested that the temporal change in soil respiration was affected not only by the seasonal change of soil temperature and soil water content but also by the biotic factors (Adachi et al., 2006).

Studies also showed that soil respiration varied with forest types (Fernandez et al., 1993), the management of forests (Raich and Schlesinger, 1992), litter-fall production (Raich and Nadelhoffer, 1989) and soil organic carbon (Adachi et al., 2006). In the present study, carbon inputs through the litter-fall were 5.30, 7.83, and 2.94 t ha^{-1} in BF, MF and PF, respectively. Since the mean annual decomposition rates of litter-fall were 49.2, 40.8 and 36.9% in BF, MF and PF, respectively, the carbon inputs were 2.61, 3.19 and 1.09 t ha⁻¹ in corresponding forests (Zhang et al., 2000). However, SOC in Table 1 showed it was the highest in BF and the lowest in PF. Whether root exudates and sloughed roots significantly contributed to SOC was unclear. Therefore, the correlation between soil respiration and SOC warrants further investigation.

4.3. Advantages and potential sources of error

Although there exists some disadvantages in the technique employed in the present study, our results showed that the combination of the trenching and the root excision method is a practical approach to separate total soil respiration into different components in the field.

The advantages and disadvantages of the techniques for separating autotrophic and heterotrophic respiration were

summarized in the previous studies (Kuzyakov and Larionova, 2005; Subke et al., 2006). In the present study, the root excision method would introduce not only physical wound to root, but also an artificial physical (no soil medium) and chemical environment (lower CO₂ concentration around roots). It is noteworthy to point out that CO₂ concentration is usually different at different soil depths, with a range of 2000-6000 ppm. We measured the root respiration under both 400 and 2500 ppm, and a correction factor was used for the root respiration correction. This would make our root respiration data more reliable; however, errors could not be excluded when only one concentration of CO₂ was considered for the whole soil profile. In some studies, high CO₂ has been shown to inhibit or alter total respiration rate (Burton et al., 1997) and maintenance respiration rate (Lipp and Andersen, 2003). In spite of the criticisms on the root excision method, it is still a common approach to measure the root respiration because it is convenient and direct. The trenching method has also been widely used to partition soil respiration into autotrophic and heterotrophic respiration (Kelting et al., 1998; Bond-Lamberty et al., 2004; Jiang et al., 2005). This method also introduces complications that are difficult to resolve. Firstly, the creation of trenching plots will disturb the soil structure, consequently, causing changes in soil temperature and soil water content. Secondly, the residual roots introduced by the trenching plots will cause the increase of soil respiration for a certain period of time, which will cause the R_{root} -to- R_{total} ratios be underestimated by 5-10% (Bond-Lamberty et al., 2004). Thirdly, the timing of the measurement is difficult to determine. Our results showed soil respiration rates reached to the relatively stable values after the plots were trenched for four months, which was consistent with Kelting et al. (1998). However, other studies suggested that the trenched plots would not reach to the equilibrium until one year after the trenching (Ewel and Cropper, 1987; Bowden et al., 1993; Bond-Lamberty et al., 2004).

Soil respiration rates and root respiration rates obtained by the dynamic chamber in the present study might be overestimated, and it is one of the most common sources of error in soil CO_2 efflux using the dynamic chamber. Firstly, the CO_2 from soil respiration in the dynamic chamber would be extracted immediately, which might cause an increase pulse of CO₂ release to atmosphere. Secondly, to calculate soil respiration rates with the dynamic chamber, the difference of CO₂ concentration between the inlet and outlet was used. CO₂ concentration of the outlet could be used only when the CO₂ concentration inside the chamber reached the equilibrium, however, it was difficult to detect such an equilibrium point in the present study, which might cause a possible over-estimation of the soil respiration rates. Although negative air pressure inside the chamber would cause the increase of soil respiration and root respiration rates, it would cause little effect on the flux comparisons between trenched and not trenched plots as the relative artifact applies to both treatments.

5. Conclusion

The present study demonstrated that soil respiration rates and root respiration rates varied significantly between the rain season and the dry season. The ratios of each component to total soil respiration varied with the forests and seasons, which could be attributed to the differences in temperature, soil water content, root biomass and soil microbial biomass. The influence of carbon input and soil organic carbon on soil respiration is still unclear in the present study and warrants further investigation. In general, our results suggested that the effects of forest types and seasons on soil respiration and the ratios of each component to total soil respiration should be taken into account in regional and global C modeling or budgeting.

Taking into account all the advantages and disadvantages, the root excision method combined with the trenching method seemed to be a practical approach for partitioning total soil respiration into three components.

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References

- Adachi, M., Bekku, Y.S., Rashidah, W., Okuda, T., Koizumi, H., 2006. Differences in soil respiration between different tropical ecosystems. Appl. Soil Ecol. 34, 258–265.
- Andersen, C.P., Nikilov, I., Nikolova, P., Matyssek, R., H\u00e4berle, K., 2005. Estimating "autotrophic" belowground respiration in spruce and beech forests decreases following girdling. Eur. J. Forest Res. 124, 155–163.
- Andrews, J.A., Harrison, K.G., Matamala, R., Schlesinger, W.H., 1999. Separation of root respiration from total soil respiration using carbon-13 labelling during free-air carbon dioxide enrichment (FACE). Soil Sci. Soc. Am. J. 63, 1429–1435.
- Bond-Lamberty, B., Wang, C., Gower, S.T., 2004. Contribution of root respiration to soil surface CO₂ flux in a boreal black spruce chronosequence. Tree Physiol. 24, 1387–1395.
- Bowden, R.D., Nadelhoffer, K.J., Boone, R.D., Melillo, J.M., Garrison, J.B., 1993. Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. Can. J. Forest Res. 23, 1402–1407.
- Bowden, R.D., Newkirk, K.M., Rullo, G., 1998. Carbon dioxide and methane fluxes by a forest soil under laboratory-controlled moisture and temperature conditions. Soil Biol. Biochem. 30, 1591–1597.
- Burton, A.J., Zogg, G.P., Pregirzer, K.S., Zak, D.R., 1997. Effect of measurement CO₂ concentration on sugar maple root respiration. Tree Physiol. 17, 421–427.
- Chen, C.R., Condron, L.M., Xu, Z.H., Davis, M.R., Sherlock, R.R., 2006. Root, rhizosphere and root-free respiration in soils under grassland and forest plants. Eur. J. Soil Sci. 57, 58–66.
- Ding, M., Brown, S., Lugo, A.E., 2001. A Continental Subtropical Forest in China Compared with an insular Subtropical Forest in the Caribbean. Gen. Tech. Rep. IIF-17. USDA, Forest Service, Institute of Tropical Forestry, Rio Piedras, PR, 46 pp.
- Ewel, K.C., Cropper, W.P., 1987. Soil CO₂ evolution in Florida slash pine plantations. II. Importance of root respiration. Can. J. Forest Res. 17, 330– 333.
- Fernandez, I.J., Son, Y., Kraske, C.R., Rustad, L.E., David, M.B., 1993. Soil carbon dioxide characteristics under different forest types and after harvest. Soil Sci. Soc. Am. J. 57, 1115–1121.
- Giardina, C.P., Ryan, M.G., 2000. Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. Nature 404, 858–861.

- Hanson, P.J., Edwards, N.T., Garten, C.T., Andrews, J.A., 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. Biogeochemistry 48, 115–146.
- He, C., Chen, S., Liang, Y., 1982. The soils of Dinghushan Biosphere Reserve. Trop. Subtrop. Forest Ecosyst. 1, 25–38 (in Chinese, with English abstract).
- Jenkinson, D.S., Powlson, D.S., 1976. The effects of biocidal treatments on metabolism in soil—V. A method for measuring soil biomass. Soil Biol. Biochem. 8, 209–213.
- Jiang, L.F., Shi, F.C., Li, B., Luo, Y.Q., Chen, J.Q., Chen, J.K., 2005. Separating rhizosphere respiration from total soil respiration in two larch plantations in northeastern China. Tree Physiol. 25, 1187–1195.
- Kane, E.S., Valentine, D.W., Schuur, E.A.G., Dutta, K., 2005. Soil carbon stabilization along climate and stand productivity gradients in black spruce forests of interior Alaska. Can. J. Forest Res. 35, 2118–2129.
- Kelting, D.L., Burger, J.A., Edwards, G.S., 1998. Estimating root respiration, microbial respiration in the rhizosphere, and root free soil respiration in forest soils. Soil Biol. Biochem. 30, 961–968.
- Kuzyakov, Y., Larionova, A.A., 2005. Root and rhizomicrobial respiration: a review of approaches to estimate respiration of autotrophic and heterotrophic organisms in soil. J. Plant Nutr. Soil Sci. 168, 503–520.
- Lee, M.S., Nakane, K., Nakatsubo, T., Koizumi, H., 2003. Seasonal changes in the contribution of root respiration to total soil respiration in a cooltemperate deciduous forest. Plant Soil 255, 311–318.
- Li, M., Wang, Z., 1984. The phenology of common plants in Ding Hu Shan. Trop. Subtrop. Forest Ecosyst. 2, 1–11 (in Chinese, with English abstract).
- Lipp, C.C., Andersen, C.P., 2003. Role of carbohydrate supply in white and brown root respiration of ponderosa pine. New Phytol. 160, 523–531.
- Melillo, J.M., Steudler, P.A., Aber, J.D., Newkirk, K., Lux, H., Bowles, F.P., Catricala, C., Magill, A., Ahrens, T., Morrisseau, S., 2002. Soil warming and carbon-cycle feedbacks to the climate system. Science 298, 2173–2176.
- Ohashi, M., Gyokusen, K., Saito, A., 2000. Contribution of root respiration to total soil respiration in a Japanese cedar (*Cryptomeria japonica* D. Don) artificial. Ecol. Res. 15, 323–333.
- Raich, J.W., Nadelhoffer, K.J., 1989. Belowground carbon allocation in forest ecosystems: global trends. Ecology 70, 1346–1354.

- Raich, J.W., Schlesinger, W.H., 1992. The global carbon dioxide flux in soil respiration and its relation to vegetation and climates. Tellus 44B, 81–99.
- Raich, J.W., Potter, C.S., 1995. Global patterns of carbon dioxide emissions from soils. Global Biogeochem. Cy. 9, 23–36.
- Raich, J.W., Potter, C.S., Bhagawati, D., 2002. Interannual variability in global soil respiration, 1980–94. Global Change Biol. 8, 800–812.
- Schlesinger, W.H., Andrews, J.A., 2000. Soil respiration and the global carbon cycle. Biogeochemistry 48, 7–20.
- Subke, J.A., Inglima, I., Cotrufo, M.F., 2006. Trends and methodological impacts in soil CO₂ efflux partitioning: a metaanalytical review. Global Change Biol. 12, 921–943.
- Sulzman, E.W., Brant, J.B., Bowden, R.D., Lajtha, K., 2005. Contribution of aboveground litter, belowground litter, and rhizosphere respiration to total soil CO₂ efflux in an old growth coniferous forest. Biogeochemistry 73, 231–256.
- Tang, J., Misson, L., Gershenson, A., Cheng, W., Goldstein, A.H., 2005. Continuous measurements of soil respiration with and without roots in a ponderosa pine plantation in the Sierra Nevada Mountains. Agric. For. Meteorol. 132, 212–227.
- Veenendaal, E.M., Kolle, O., Lloyd, J., 2004. Seasonal variation in energy fluxes and carbon dioxide exchange for a broad-leaved semi-arid savanna (Mopane woodland) in Southern Africa. Global Change Biol. 10, 318– 328.
- Vogt, K.A., Vogt, D.J., Palmiotto, P.A., Boon, P., O'Hara, J., Asbjornsen, H., 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant Soil 187, 159–219.
- Wang, Z., He, D., Song, S., Chen, S., Chen, D., Tu, M., 1982. The vegetation of Dinghushan Biosphere Reserve. Trop. Subtrop. Forest Ecosyst. 1, 77–141 (in Chinese, with English abstract).
- Zhang, D., Ye, W., Yu, Q., Kong, G., Zhang, Y., 2000. The litter-fall of representative forests of successional series in Dinghushan. Acta Ecol. Sin. 20, 938–944 (in Chinese, with English abstract).
- Zhang, Z., Ding, M., 1996. Biomass and efficiency of radiation utilization in monsoon evergreen broadleaved forest in Dinghushan Biosphere Reserve. Acta Ecol. Sin. 16, 525–534 (in Chinese, with English abstract).