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Soil-atmospheric exchange of CO_2, CH_4, and N_2O in three subtropical forest ecosystems in southern China

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Abstract

The magnitude, temporal, and spatial patterns of soil-atmospheric greenhouse gas (hereafter referred to as GHG) exchanges in forests near the Tropic of Cancer are still highly uncertain. To contribute towards an improvement of actual estimates, soil-atmospheric CO_2, CH_4, and N_2O fluxes were measured in three successional subtropical forests at the Dinghushan Nature Reserve (hereafter referred to as DNR) in southern China. Soils in DNR forests behaved as N_2O sources and CH_4 sinks. Annual mean CO_2, N_2O, and CH_4 fluxes (mean $\pm$ SD) were 7.7 ± 4.6 Mg CO_2-C ha^{-1} yr^{-1}, 3.2 ± 1.2 kg N_2O-N ha^{-1} yr^{-1}, and 3.4 ± 0.9 kg CH_4-C ha^{-1} yr^{-1}, respectively. The climate was warm and wet from April through September 2003 (the hot-humid season) and became cool and dry from October 2003 through March 2004 (the cool-dry season). The seasonality of soil CO_2 emission coincided with the seasonal climate pattern, with high CO_2 emission rates in the hot-humid season and low rates in the cool-dry season. In contrast, seasonal patterns of CH_4 and N_2O fluxes were not clear, although higher CH_4 uptake rates were often observed in the cool-dry season and higher N_2O emission rates were often observed in the hot-humid season. GHG fluxes measured at these three sites showed a clear increasing trend with the progressive succession. If this trend is representative at the regional scale, CO_2 and N_2O emissions and CH_4 uptake in southern China may increase in the future in light of the projected change in forest age structure. Removal of surface litter reduced soil CO_2 effluxes by 17–44% in the three forests but had no significant effect on CH_4 absorption and N_2O emission rates. This suggests that microbial CH_4 uptake and N_2O production was mainly related to the mineral soil rather than in the surface litter layer.

Keywords: Dinghushan Nature Reserve, GHG fluxes, seasonal difference, soil-atmospheric exchange, succession stage, successional forests

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Introduction

The increase of greenhouse gas (GHG) in the atmosphere has led to a warming of the Earth's surface and other climate changes since the Preindustrial Era (ca. 1750 AD). According to the Intergovernmental Panel on Climate Change (IPCC, 2001), the globally averaged atmospheric concentrations of CO_2, CH_4, and N_2O are increasing at rates of 1.5 ppm yr^{-1}, 7.0, and 0.8 ppb yr^{-1}, respectively. These increases are attributed mainly to anthropogenic activities, such as deforestation, agricultural practices, and burning of fossil fuels (IPCC, 1995). Besides, a considerable amount of atmospheric GHG is produced and consumed through soil processes. As a major pathway in the global carbon cycle, the flux of carbon from soils to the atmosphere in the form of CO_2 is estimated to have a magnitude of 68–100 Pg C yr^{-1} (Musselman & Fox, 1991; Raich & Schlesinger, 1992). It is second only to gross primary productivity (100–120 Pg C yr^{-1}) (Houghton & Woodwell, 1989). Soil N_2O emissions accounted for about 57% of global atmospheric sources of N_2O (Breuer *et al*., 2000). Nonflooded soils, the only biological sink of atmospheric CH_4, are responsible for 6% of the global CH_4 consumption, corresponding to 30 Tg yr^{-1} (Le Mer & Roger, 2001;

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Bodelier & Laanbroek, 2004). The increasing atmospheric GHG concentrations have raised concerns about potential global warming and the possible positive feedback effects that warming could have on further fluxes between soil and atmosphere (Mosier, 1998; Rustad *et al*., 2000). Most of the studies on soil-atmospheric GHG exchange were conducted in temperate forests in mid- to high-latitude regions (e.g. Raich & Schlesinger, 1992; Janssens *et al*., 2001; Davidson *et al*., 2002a; Reichstein *et al*., 2003) and tropical forests (e.g. Bouwman, 1998; Breuer *et al*., 2000; Verchot *et al*., 2000; Veldkamp *et al*., 2001; Kiese & Butterbach-Bahl, 2002; Kiese *et al*., 2003, 2005). To our knowledge, few reports are available on soil-atmospheric GHG exchanges in forests close to the Tropic of Cancer.

Because of its position near the Pacific Ocean in the east and the Indian Ocean in the south, southern China has a subtropical monsoon climate with an abundance of heat, light, and water resources (Ding *et al*., 2001). Because of its unique climate regime, moist subtropical forests spread out in southern China, although a large area near the Tropic of Cancer is covered by deserts (Kong *et al*., 1993). Forests in this region, therefore, deserve more attention with the respect to climate change. In light of the dynamic nature of forest age structure, it is also important to understand GHG soil emissions from forests at different successional stages. Moreover, knowledge of temporal patterns of soil GHG fluxes, as well as the climatic and environmental controls in these forests, is necessary for upscaling GHG fluxes to the regional scale. Forests in the Dinghushan Nature Reserve (DNR), including typical forests in southern China from early-, mid-, to advanced-successional stages, provide an excellent opportunity to study these issues.

Forests in southern China have been impacted by human activities, including timber and intensive biofuel harvesting, for hundreds of years (Brown *et al*., 1995). Although the practice of litter harvesting has declined dramatically in the study region because of economic development and shifting in fuel sources, the impact of litter removal on GHG fluxes has never been studied in southern China. Studies in other biomes have found that soil surface litter removal had a negative impact on soil GHG fluxes (Dong *et al*., 1998; Rey *et al*., 2002; Li *et al*., 2004). In this paper, we analyze the CO_2, CH_4, and N_2O flux data observed from three typical subtropical forests at the DNR. These forests were selected to form a successional sequence. Our null hypothesis is that the seasonal patterns and annual GHG fluxes among these forests were the same, without dependence on successional stages. In addition, GHG flux measurements were made with and without surface litter from the forest floor to test the null hypothesis that litter removal does not affect GHG fluxes in these forests. Our specific aims were to (1) observe seasonal variations of CO_2, CH_4, and N_2O fluxes according to forest; (2) estimate the contribution of litter to GHG fluxes; and (3) evaluate the relationship between soil-atmospheric GHG exchange and soil temperature and moisture.

Methods

Site description

The DNR, with an area of 1133 ha and an elevation ranging from 10 to 1000 m above sea level, is located in the mid-part of Guangdong Province in south China (112°30′39″–112°33′41″E, 23°09′21″–23°11′30″N). The region is characterized by a typical south subtropical monsoon climate, with annual average precipitation of 1927 mm, of which nearly 80% falls in the hot-humid season (April–September) and 20% in the cool-dry season (October–March). The annual mean temperature is 21.4 °C, and the relative humidity is 80%. Bedrocks are classified as Devonian sandstone and shale (Wu *et al*., 1982). Soils are classified as lateritic red earth (oxisol), loamy in texture, and acidic (the pH value of the top 20 cm soil layer was about 3.9 (Ding *et al*., 2001)), with low base saturation (He *et al*., 1982).

In this study, three plots, each representing a common forest type, were chosen within the DNR. The three forests, including pine forest, conifer, and broadleaf mixed forest (hereafter referred to as mixed forest), and evergreen broadleaf forest (hereafter referred to as broadleaf forest), represent forests in early-, mid-, and advanced-successional stages in the region (Peng & Wang, 1985, 1995). During natural succession, heliophytes (e.g. *Schima superba* and *Castanopsis chinensis*) gradually invade pine forests to form mixed forests, and mesophytes (e.g. *Cryptocarya concinna*, *Cryptocarya chinensis*) subsequently invade mixed forests and eventually transform them into evergreen broadleaf forests.

Pine forest, which was originally planted by local people in the 1930s, is distributed primarily in the hilly lands of the eastern, southern, and northern portions of the reserve, with an elevation of 50–200 m. It has a long history of human disturbances because it is easily accessible by nearby villagers. Local people used to harvest trees, shrubs, and surface litter for fuel. Since the 1950s, people have been restricted from cutting trees but were allowed to harvest other forms of biomass, such as litter and shrubs, from the pine forest. Litter harvesting did not cease until 1990. Pine forest is dominated by *Pinus massoniana* in the tree layer and *Rhodomyrtus tomentosa*, *Dicranopteris linearis*, and *Baeckea frutescens* in the shrub and herb layers.

Mixed forest was developed from artificial pine forest with a gradual invasion of some pioneer broadleaf species through natural succession. Because the mixed forest was free from human impact for about 70 years, its species composition is different from that of the pine forest of the same age. Dominant species in the mixed forest include *P. massoniana*, *S. superba*, *C. chinensis*, and *Craibiodendron kwangtungense*.

Broadleaf forest is the regional climax vegetation. It is distributed at an elevation that varies from 250 to 350 m. Located around a temple built in 1633 AD, the broadleaf forest has been well protected from human disturbance for more than 400 years by Buddhist monks. Dominant species in the broadleaf forest include *C. chinensis*, *C. chinensis*, *C. concinna*, *Erythrophleum fordii*, and *Cyathea podophylla* (Kong *et al*., 1993). The main characteristics of the forests are listed in Table 1.

Experimental design

Six chambers were installed at each forest site in February 2003. At each site, three chambers were randomly designated to measure the impacts of surface litter exclusion (i.e. the bare soil or 'BS' treatment), and the rest were used as the control (i.e. soil with surface litter or 'SL' treatment). For the BS treatment, litter was removed carefully at least 1 hr before each sampling. Contribution of litter to GHG fluxes was estimated using the following equation:

$$Contribution = \frac{F_c - F_t}{F_c} \times 100\% \qquad (1)$$

where *Contribution* stands for the contribution of surface litter to total soil-atmosphere GHG flux, and F_c and F_t stand for CO_2, N_2O, or CH_4 flux measured from control (SL) treatment and litter exclusion (BS) treatment, respectively.

Field measurements were carried out weekly in the broadleaf forest and the mixed forest, and biweekly in the pine forest. The pine forest plot, located far away from the broadleaf forest and the mixed forest plots, prevented us from collecting field data with the same frequency as in the other forests.

Flux measurements

Fluxes of CO_2, CH_4, and N_2O were measured using static chamber and gas chromatography techniques (Wang & Wang, 2003). The static chamber was made of stainless-steel and consisted of two parts, a square box (without a top and bottom, length × width × height = 0.5 m × 0.5 m × 0.1 m) and a removable cover box (without bottom, length × width × height = 0.5 m × 0.5 m × 0.5 m). The square box was inserted directly into the forest floor about 10 cm below the floor surface, and the cover was placed on top during sampling and removed afterwards. A fan 10 cm in diameter was installed on the top wall of each chamber to make turbulence when chamber was closed. Using a fan may have caused a bias in measurements by altering concentration gradients (see Le Dantec *et al*., 1999;

Table 1 Stand characteristics of three forests in Dinghushan Nature Reserve

Forest	Pine forest	Mixed forest	Broadleaf forest
Successional stage	Early	Mid	Advanced
Biomass ($Mg\,C\,ha^{-1}$)*	40.6	116.2	147.8
Microbial biomass ($\times 10^6\,g^{-1}$dry soil)†	1.2	1.4	2.1
Fine root biomass in top soil ($Mg\,C\,ha^{-1}$)‡	1.9 (1.1)	2.8 (1.1)	4.9 (3.0)
Litter input ($Mg\,C\,ha^{-1}\,yr^{-1}$)§	1.8	4.3	4.2
SOC¶ ($Mg\,C\,ha^{-1}$)	105.2	111.3	164.1
pH‖	4.02	3.92	3.80
Bulk density ($g\,cm^{-3}$)‖	1.495	1.220	1.093
NO_3^--N content ($mg\,kg^{-1}$)‖	4.0	4.8	5.8
NH_4^+-N content ($mg\,kg^{-1}$)‖	18.5	13.8	11.6
Field capacity ($cm^3\,H_2O\,cm^{-3}$ soil × 100)**	38	36	49

*From Peng & Zhang (1994, 1995); Wen *et al*. (1998).
†From Zhou *et al*. (2002)
‡Fine root in top soil refers to root (diameter less than 6 mm) biomass in 0–20 cm depth of soil. Means from eight soil drills, 10 cm in diameter, standard deviations in parentheses. Unpublished data from Dinghushan Forest Ecosystem Research Station, 2003.
§Zhou *et al*. (2005, in press).
¶From Fang *et al*. (2003). SOC stocks were accounted to a depth of 60 cm.
‖Mean concentrations from 20 samples for each forest. Soil sample were collected in July 2003 using soil drills (10 cm in diameter) from 0 to 20 cm depth of soil. Unpublished data from Dinghushan Forest Ecosystem Research Station, 2003.
**From Zhang & Zhuo (1985).

Davidson *et al.*, 2002b). No vent was installed in the chamber, which may have introduced artifacts in flux measurements owing to pressure differentials between the inside and outside of the chamber caused by circulating gases or by cooling or warming of chamber air (see Davidson *et al.*, 2002b). White adiabatic cover was added outside of the stainless steel cover to reduce the impact of direct radiative heating during sampling. A typical measurement started at 09:00 hours and lasted for about 30 min. Our diurnal studies demonstrated that GHG fluxes measured at 09:00 hours were close to daily means (Fig. 1). Gas samples (100 mL each) were collected every 10 min using 100 mL plastic syringes.

CO_2, CH_4, and N_2O concentrations in the samples were analyzed in the laboratory within 24 h following sampling using gas chromatography. The gas chromatography was equipped with an electron capture detector for N_2O analysis and a flame ionization detector for CH_4 and CO_2 analysis. The gas chromatography configurations for analyzing concentrations of CO_2, CH_4, and N_2O and the methods for calculating the fluxes of each gas were the same as those described by Wang & Wang (2003). GHG flux was calculated based on the rate of change in GHG concentration within the chamber, which was estimated as the slope of linear regression between concentration and time. All the coefficients of determination (r^2) of the linear regression were greater than 0.98 in our study.

Soil temperature and moisture measurements

Soil temperature and moisture at 5 cm below soil surface were monitored at each chamber simultaneously while gas samples were collected. Soil temperature was measured using digital thermometers. Volumetric soil moisture (cm^3 $H_2O\,cm^{-3}$ soil) was measured using a MPKit (ICT, Australia, see http://www.ictinternational.com.au/soils.htm), which consists of three amplitude domain reflectometry (ADR) moisture probes (MP406) and a data logger (MPM160 meter). Volumetric soil moisture contents, determined automatically by the MPKit using vendor-supplied generalized calibrations, were read directly from the display of the MPM160 meter.

Climatic data (precipitation and air temperature) were obtained from the weather station at the Dinghushan Forest Ecosystem Research Station, part of the Chinese Ecosystem Research Network.

Statistical analysis

Daily mean GHG fluxes, soil temperature, and soil moisture for each treatment were calculated by averaging the three replicates for each sampling day. Analyses of variance (ANOVA) were performed using daily means to test the difference of soil temperature, soil moisture, and GHG fluxes by season, surface litter treatment (BS and SL), and forest. A full general linear model (GLM in SAS) in which forest type was treated as an independent variable was used to compare the differences of environmental factors and GHG fluxes among the three forests, and to assess the significance of the impacts of forest, season, surface litter removal, and their interactions on GHG fluxes. In addition, a reduced GLM model was developed for each forest to assess the significance of the effects of season, surface litter treatment, and their interactions on GHG fluxes.

The relationships between GHG fluxes and soil temperature and soil moisture were examined using model fitting. Both linear and nonlinear regression models were fitted. Mean standard error (MSE), R^2 (for linear model), pseudo-R^2 (for nonlinear model) (Helland,

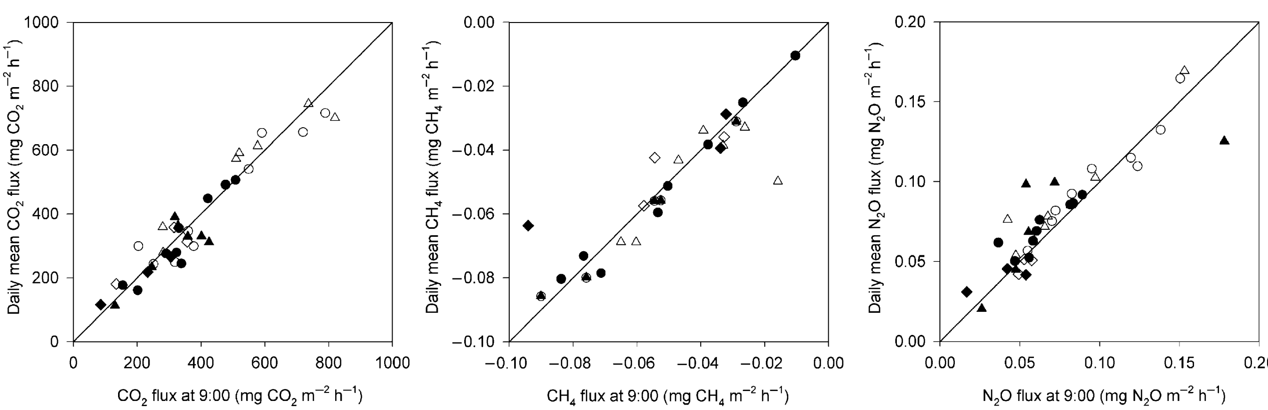

Fig. 1 Correlations between greenhouse gas (GHG) fluxes measured at 09:00 hours and daily means in the pine (diamonds), mixed (triangles), and broadleaf (circles) forest. Daily means were calculated by averaging GHG fluxes from 10 measurements in diurnal observations. Open and closed symbols represent GHG flux measured from the control (SL) and the litter exclusion (BS) treatment, respectively.

1987; Motulsky & Christopoulos, 2003), and the 95% confidence interval of the model parameters were used to determine goodness-of-fit. A P-value <0.05 was used to reject the null hypothesis that the model is not significant.

Results

Environmental factors

Precipitation from April 2003 to March 2004 was 1429 mm, less than the long-term average annual rainfall of 1927 mm (Wu *et al.*, 1982). Intense rainstorms occurred in June, August, and September 2003. Precipitation during these 3 months accounted for more than 60% of total rainfall throughout the observation period. Winter was relatively dry with only 0.1 mm precipitation from November to December 2003. Annual air temperature was 19.7 °C, with monthly temperature ranging from 10.9 °C (January 2004) to 27.6 °C (July 2003) (Fig. 2a).

Soil temperature and moisture exhibited clear seasonal courses. Soil was warm and wet from April through September 2003 (the hot-humid season) and became cool and dry from October 2003 through March 2004 (the cool-dry season) (Fig. 2b and c). The seasonality of soil temperature and moisture is consistent with the seasonal patterns of air temperature and precipitation (Fig. 2). Soil in the pine forest was significantly drier than that in the mixed forest and the broadleaf forest ($P<0.05$) (Tables 2 and 3, and Fig. 2c). Removal of the litter layer did not alter the regimes of soil temperature in all forests (Table 3). Litter removal had a significant impact on soil moisture in the mixed forest ($P<0.0001$) but not in the broadleaf forest and the pine forest ($P>0.05$) (Table 4).

Seasonality of GHG fluxes

In all forests, CO_2 emission rates were significantly higher in the hot-humid season (April–September 2003) than in the cool-dry season (October 2003–March 2004) ($P<0.0001$) (Fig. 3, Tables 2 and 3). Maximum CO_2 release took place in July 2003 when soil temperature was relatively high and humidity was moderate, while minimum emissions occurred in winter when both soil temperature and moisture were low (Fig. 3). Seasonal difference of CO_2 emissions was more pronounced in the control (SL) treatment than in the litter exclusion (BS) treatment within all forests.

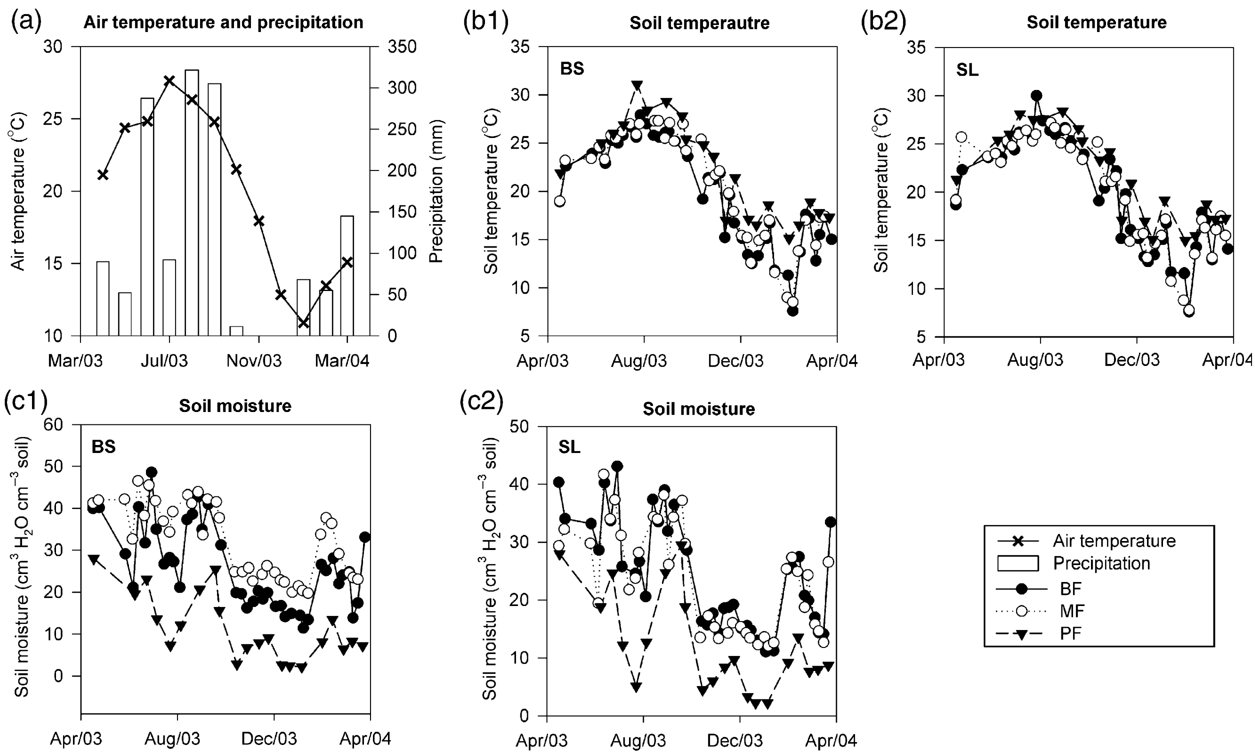

Fig. 2 Seasonal patterns of air temperature and precipitation (a), soil temperature (B1 and B2), and volumetric soil moisture (C1 and C2) measured in three forests with (BS) or without (SL) surface litter exclusion. Each datum in panels B1, B2, C1, and C2 is the mean of three replications. BF, broadleaf forest; MF, mixed forest; PF, pine forest.

Table 2 Effects of surface litter removal (BS, bare soil; SL, soil with surface litter) on the mean value (± standard error) of soil temperature, moisture, and greenhouse gas fluxes from forest soils in Dinghushan Nature Reserve

Forest		Broadleaf forest		Mixed forest		Pine forest	
Treatment		BS	SL	BS	SL	BS	SL
Soil temperature (°C)	Cool-dry season	15.7 ± 0.8	15.8 ± 0.8	16.4 ± 1.0	16.0 ± 0.9	18.2 ± 0.7	18.4 ± 0.9
	Hot-humid season	24.9 ± 0.5	25.0 ± 0.6	25.3 ± 0.5	24.9 ± 0.4	26.9 ± 0.9	26.2 ± 0.7
	Annual mean	19.9 ± 0.9	19.7 ± 0.9	20.3 ± 0.9	20.1 ± 0.9	22.1 ± 1.1	21.8 ± 1.0
Soil moisture (cm^3 H_2O cm^{-3} soil)	Cool-dry season	19.5 ± 1.2	17.8 ± 1.2	25.4 ± 1.1	16.5 ± 1.0	6.8 ± 1.0	6.9 ± 1.0
	Hot-humid season	34.2 ± 1.8	32.8 ± 1.5	40.2 ± 1.0	31.3 ± 1.4	18.4 ± 2.2	19.4 ± 2.7
	Annual mean	26.1 ± 1.6	24.2 ± 1.5	31.9 ± 1.5	23.3 ± 1.5	12.0 ± 1.7	12.3 ± 1.9
CO_2 flux (mg CO_2 m^{-2} h^{-1})	Cool-dry season	236 ± 14.1	302 ± 18.4	125 ± 15.9	231 ± 14.8	97.4 ± 7.0	131 ± 10.0
	Hot-humid season	524 ± 39.6	705 ± 40.1	364 ± 27.5	589 ± 22.0	283 ± 14.4	402 ± 26.9
	Annual mean	366 ± 29.9	473 ± 37.6	231 ± 24.9	396 ± 31.7	181 ± 22.4	2471 ± 32.5
CH_4 flux (mg CH_4 m^{-2} h^{-1})	Cool-dry season	0.083 ± 0.008	0.105 ± 0.008	0.065 ± 0.009	0.067 ± 0.006	0.062 ± 0.006	0.070 ± 0.020
	Hot-humid season	0.097 ± 0.019	0.070 ± 0.006	0.057 ± 0.005	0.060 ± 0.006	0.048 ± 0.005	0.046 ± 0.002
	Annual mean	0.089 ± 0.009	0.089 ± 0.006	0.059 ± 0.005	0.063 ± 0.004	0.054 ± 0.007	0.057 ± 0.010
N_2O flux (mg N_2O m^{-2} h^{-1})	Cool-dry season	0.054 ± 0.005	0.063 ± 0.006	0.030 ± 0.003	0.049 ± 0.008	0.034 ± 0.005	0.048 ± 0.004
	Hot-humid season	0.087 ± 0.011	0.109 ± 0.012	0.089 ± 0.010	0.063 ± 0.008	0.034 ± 0.008	0.049 ± 0.011
	Annual mean	0.069 ± 0.006	0.084 ± 0.007	0.058 ± 0.007	0.056 ± 0.006	0.034 ± 0.004	0.048 ± 0.006

Positive CH_4 values are CH_4 uptake.

CH_4 measurements indicated a consistent net soil consumption of CH_4 (i.e. negative CH_4 flux) in the three forests (Fig. 3). Seasonality had no significant impact on CH_4 uptake (Fig. 3 and Table 3). ANOVA suggested no significant seasonal difference ($P > 0.05$) in CH_4 uptake in all forests (Table 3), although higher uptake rates were observed in the cool-dry season.

Soils were N_2O sources (Fig. 3). Clear seasonality of N_2O emissions was found in both treatments at the broadleaf forest and in the litter exclusion (BS) treatment at the mixed forest. ANOVA showed a significant seasonal difference in N_2O emissions ($P < 0.0001$) in these three cases, while no significant seasonal variation ($P > 0.05$) was found in other cases (Tables 2–4).

Influences of soil surface litter on GHG fluxes

Generally, removal of the litter layer reduced soil CO_2 efflux (Fig. 3 and Tables 2–4). ANOVA showed that the effect of surface litter removal was significant ($P < 0.0001$) across all forests (Tables 3 and 4). On average, the contributions of the litter layer to CO_2 efflux, calculated using (1), were 17%, 44%, and 23% of the CO_2 effluxes from the forest floor in the broadleaf forest, the mixed forest, and the pine forest, respectively. In contrast, litter removal did not affect either CH_4 uptake rates or N_2O release rates within each forest ($P > 0.05$) (Tables 3 and 4).

Forest succession stage and GHG fluxes

CO_2 emissions showed an increasing trend with the progression of succession. CO_2 effluxes measured in the broadleaf forest were significantly higher than those in the mixed forest and the pine forest ($P < 0.001$) (Fig. 3, Tables 2 and 3). Annual mean CO_2 emission rates derived from the litter exclusion (BS) treatment in the mixed forest and the pine forest were not different from each other ($P > 0.05$), while those from the control (SL) treatment were significantly higher in the mixed forest than in the pine forest ($P < 0.05$) (Tables 2 and 3).

The broadleaf forest soil assimilated significantly more CH_4 than the mixed forest and the pine forest soils regardless of litter removal ($P < 0.05$) (Tables 2 and 3). However, the difference in CH_4 uptake rates between the mixed forest and the pine forest was not significant ($P > 0.05$) (Table 2).

N_2O emissions were significantly different among the forests (Tables 2 and 3), with the highest rates in the broadleaf forest, followed by the mixed forest and the pine forest (Table 2). N_2O emissions in the hot-humid season were significantly higher than those in the cool-dry season in the broadleaf forest and the mixed forest ($P < 0.05$), but not in the pine forest (Tables 2 and 4).

Table 3 Significance of the impacts of forest type, litter removal treatment, season, and their interactions on soil temperature, moisture, and soil-atmospheric greenhouse exchanges at the Dinghushan Nature Reserve

	Soil temperature	Soil moisture	CO_2	N_2O	CH_4
Forest	*	**	**	**	**
Treatment	ns	*	**	ns	ns
Forest × treatment	ns	**	ns	*	ns
Season	**	**	**	**	ns
Forest × season	ns	ns	ns	ns	ns
Treatment × season	ns	ns	*	ns	ns
Forest × treatment × season	ns	ns	ns	ns	ns

*Significant impact at $\alpha < 0.05$, and
**Significant impact at $\alpha < 0.0001$.
ns, no significant impact.

Table 4 Significance of the impacts of litter removal treatment, season, and their interactions on soil temperature, moisture, and soil-atmospheric greenhouse exchanges within each of the three forests at the Dinghushan Nature Reserve. All CH_4 models were not significant at $\alpha = 0.05$ and not shown in the table

Forest	Variables	Treatment	Season	Treatment*season
Broadleaf forest	Soil temperature	ns	**	ns
	Soil moisture	ns	**	ns
	CO_2	**	**	ns
	N_2O	ns	*	ns
Mixed Forest	Soil temperature	ns	**	ns
	Soil moisture	**	**	ns
	CO_2	**	**	*
	N_2O	ns	*	*
Pine Forest	Soil temperature	ns	**	ns
	Soil moisture	ns	**	ns
	CO_2	**	**	*
	N_2O	ns	ns	ns

*Significant impact at $\alpha < 0.05$, and **Significant impact at $\alpha < 0.0001$.
ns, no significant impact.

Impacts of soil temperature and moisture

The relationship between soil temperature and the CO_2 emission rate for each treatment was fitted with an exponential model and results are given in Table 5. Soil temperature explained more than 50% of CO_2 efflux variation (Table 5a and Fig. 4). Note that the relationship between CO_2 efflux and soil temperature was simultaneously affected by soil moisture because of the covariation between soil temperature and soil moisture. Unlike the exponential relationship between CO_2 efflux and soil temperature, CO_2 efflux and soil moisture had a positive linear relationship (Fig. 4). Although the relationships between CO_2 emissions and soil moisture were weaker than or comparable with those between CO_2 and soil temperature, they were significant ($P < 0.0001$), explaining 29–66% of CO_2 variations (Table 5b). A model that combines an exponential component (CO_2 emission rate and soil temperature) and linear component (CO_2 emission rate and soil moisture) yielded higher R^2 values and lower residuals than the exponential or linear model alone (Table 5c).

CH_4 fluxes did not display any pronounced dependency on soil temperature, moisture, or their interaction ($P > 0.05$), although higher CH_4 uptake rates were observed when both soil temperature and soil moisture were relatively low.

Soil temperature, as measured in this study, did not affect soil N_2O emissions distinctly ($P > 0.05$). N_2O effluxes were weakly linearly related to soil moisture. Nevertheless, the dependency of N_2O emission rate on soil moisture was different among forests (Fig. 5). N_2O fluxes measured from both the litter exclusion (BS) treatment and the control (SL) treatment in the broadleaf forest were slightly positively correlated with

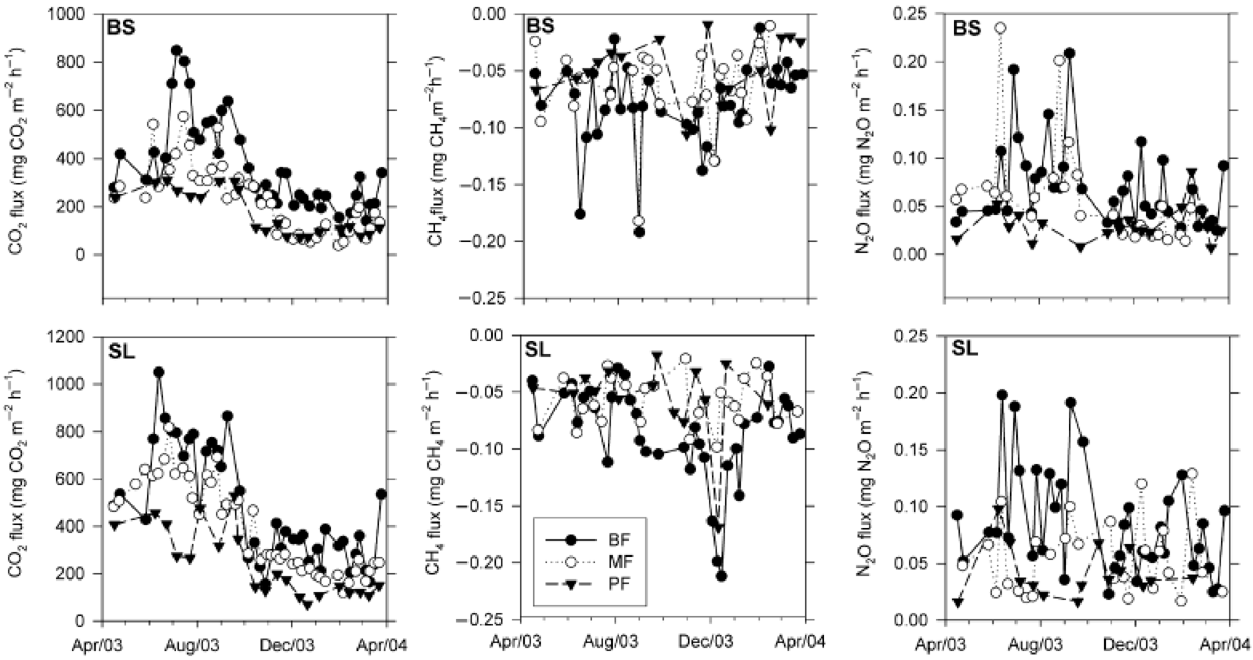

Fig. 3 Seasonal patterns of CO_2, CH_4, and N_2O fluxes measured in three forests. Each datum is mean of three replications. Meanings of abbreviations and symbols are the same as in Fig. 2.

changes in soil moisture ($R^2 = 0.20$ and 0.32, respectively). A linear model based on soil moisture explained 55% of the temporal variation of N_2O emission rates measured from the litter exclusion (BS) treatment in the mixed forest. These three treatments where soil moisture was significantly correlated with N_2O efflux also exhibited the highest efflux rates. No significant relationship was found between soil moisture and N_2O flux from the control (SL) treatment in the mixed forest, as well as from both treatments in the pine forest ($P > 0.05$), where lower efflux rates generally were measured.

Discussions

Comparisons with other studies

Annual mean soil CO_2 emissions (mean ± SD) were 9.9 ± 4.6, 7.8 ± 4.3, and $5.1 \pm 3.0\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$, respectively, from the broadleaf forest, the mixed forest, and the pine forest. On average, soils in the DNR released about $7.7 \pm 4.6\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ (mean ± SD, arithmetic average of the three sites) in the form of CO_2 into the atmosphere. The results presented here fall in the range of soil CO_2 emission rates reported by a number of similar studies worldwide (e.g. Raich, 1998; Granier *et al*., 2000; Longdoz *et al*., 2000; Raich & Tufekcioglu, 2000; Davidson *et al*., 2002a; Giardina & Ryan, 2002; Salimon *et al*., 2004; Sotta *et al*., 2004).

Forest soils have been reported as efficient CH_4 sinks (Keller *et al*., 1986; Steudler *et al*., 1989; Whalen & Reeburghn, 1990; Yavitt *et al*., 1990; Whalen *et al*., 1992). Our study showed that soils in the DNR were methane sinks with an annual mean CH_4 uptake (mean ± SD) of $3.4 \pm 0.9\,\mathrm{kg\,CH_4\text{-}C\,ha^{-1}\,yr^{-1}}$, which is comparable with that of other temperate and tropical forest soils that are not heavy clays (Steudler *et al*., 1996; Castro *et al*., 2000; Borken *et al*., 2003; Merino *et al*., 2004).

The annual mean N_2O emission (mean ± SD) from DNR forests was $3.2 \pm 1.2\,\mathrm{kg\,NO_2\text{-}N\,ha^{-1}\,yr^{-1}}$, which is within the range of N_2O fluxes in various temperate forests (Dong *et al*., 1998), and tropical forests in Australia (Kiese & Butterbach-Bahl, 2002), eastern Amazonia (Verchot *et al*., 1999), and Puerto Rico (Erickson *et al*., 2001).

Forest succession stage and GHG fluxes

Annual mean values of GHG fluxes (Table 2) demonstrated that soil-atmospheric GHG exchanges increase with progressive succession. This is consistent with similar studies in temperate and tropical forests (Verchot *et al*., 1999, 2000; Wiseman & Seiler, 2004). Soil-atmospheric CO_2 efflux, as the result of soil respiration, generates mainly from autotrophic (root) and heterotrophic (microbial) activity (Janssens *et al*., 2001). Autotrophic respiration strongly depends on the amount of living root biomass, and heterotrophic

Table 5 Models for the relationship between the soil CO_2 emissions, soil temperature (T) in °C, taken 5 cm below soil surface, and soil moisture content (cm^3 H_2O cm^{-3} soil) (%) of the top 5 cm soil layer. Values in parentheses are standard errors

Forest	Treatment	m	n	P	Pseudo-R^2	MSE
(a) $F_{CO_2} = m \times e^{(n \times T)}$						
Broadleaf forest	BS	58.6 (15.4)	0.087 (0.011)	<0.0001	0.69	11284.7
Broadleaf forest	SL	114.8 (30.9)	0.068 (0.011)	<0.0001	0.51	27718.6
Mixed forest	BS	22.2 (8.3)	0.108 (0.015)	<0.0001	0.73	6130.6
Mixed forest	SL	63.2 (15.1)	0.087 (0.009)	<0.0001	0.75	9617.8
Pine forest	BS	30.5 (13.4)	0.078 (0.017)	<0.0001	0.60	4272.6
Pine forest	SL	26.8 (15.5)	0.098 (0.022)	<0.0001	0.58	9738.7

Forest	Treatment	α	β	P	R^2	MSE
(b) $F_{CO_2} = \alpha \times M + \beta$						
Broadleaf forest	BS	10.2 (2.5)	94.9 (71.4)	0.0003	0.29	25 380
Broadleaf forest	SL	17.3 (2.7)	45.4 (70.9)	<0.0001	0.52	27 432
Mixed forest	BS	9.7 (2.3)	−80.9(76.9)	0.0002	0.34	14 877
Mixed forest	SL	16.0 (2.3)	21.9 (59.0)	<0.0001	0.55	17 640
Pine forest	BS	10.5 (1.8)	54.6 (25.2)	<0.0001	0.66	3605.1
Pine forest	SL	13.3 (2.6)	84.4 (38.8)	<0.0001	0.57	9947.7

Forest	Treatment	a	b	c	P	Pseudo-R^2	MSE
(c) $F_{CO_2} = ae^{(b \times T)} + c \times M$							
Broadleaf forest	BS	34.1 (19.4)	0.10 (0.02)	2.8 (2.0)	<0.0001	0.70	11 017.5
Broadleaf forest	SL	11.4 (15.2)	0.13 (0.04)	12.0 (2.5)	<0.0001	0.69	17 946.3
Mixed forest	BS	17.4 (14.9)	0.11 (0.03)	0.62 (1.63)	<0.0001	0.73	6280.2
Mixed forest	SL	23.5 (13.2)	0.11 (0.02)	6.6 (1.8)	<0.0001	0.82	7201.3
Pine forest	BS	8.3 (6.4)	0.10 (0.03)	7.5 (1.5)	<0.0001	0.85	1718.8
Pine forest	SL	9.5 (9.0)	0.12 (0.03)	8.8 (2.3)	<0.0001	0.77	5605.5

respiration depends on the quantity of dead roots and soil organic matter (Rustad *et al*., 2000). The biomass and fine root biomass patterns in our forests (Table 1) showed a tendency of increased carbon allocation to roots with progressive successional stages. The microbial biomass along successional stages (Table 1) suggested that heterotrophic increased with forest succession. This evidence indicates that the increasing CO_2 efflux between soil and atmosphere in DNR forests is the result of both enhanced autotrophic and enhanced heterotrophic respiration with progressive succession.

CH_4 flux is influenced by methanotrophs activity and soil properties, including soil diffusivity, pH (Verchot *et al*., 2000), NH_4^+-N content (Steudler *et al*., 1989; Bodelier & Laanbroekb 2004; Merino *et al*., 2004), soil organic matter (Merino *et al*., 2004), soil moisture (Castro *et al*., 1994, 2000; Bowden *et al*., 1998), and soil temperature (Castro *et al*., 1995). Lowest bulk density in the broadleaf forest (Table 1) suggested that soil diffusivity in this forest is superior to that in the mixed forest and the pine forest, leading to increased CH_4 oxidation in the broadleaf forest.

N_2O fluxes were influenced by soil moisture (Davidson, 1991; Verchot *et al*., 1999; Merino *et al*., 2004), as well as by inorganic N concentrations (Merino *et al*., 2004). Comparisons of means and amplitudes of soil moisture (Table 2) and differences of NO_3^--N contents (Table 1) among the three forests suggest that low N_2O flux in the pine forest was related to the low soil NO_3^- concentration and soil water content in the forest. This is consistent with a similar study in humid temperate regions of southern Europe where N_2O production was limited by soil water content and NO_3^- concentration. In those forests, the highest N_2O emission rates coincided with the highest amount of NO_3^--N and soil moisture and always took place when the soil moisture was higher than 25% (Merino *et al*., 2004).

The statistical analyses in this paper are based on replicate chamber measurements within each forest rather than based on true replication of forests at each successional stage. Because of the pseudoreplication,

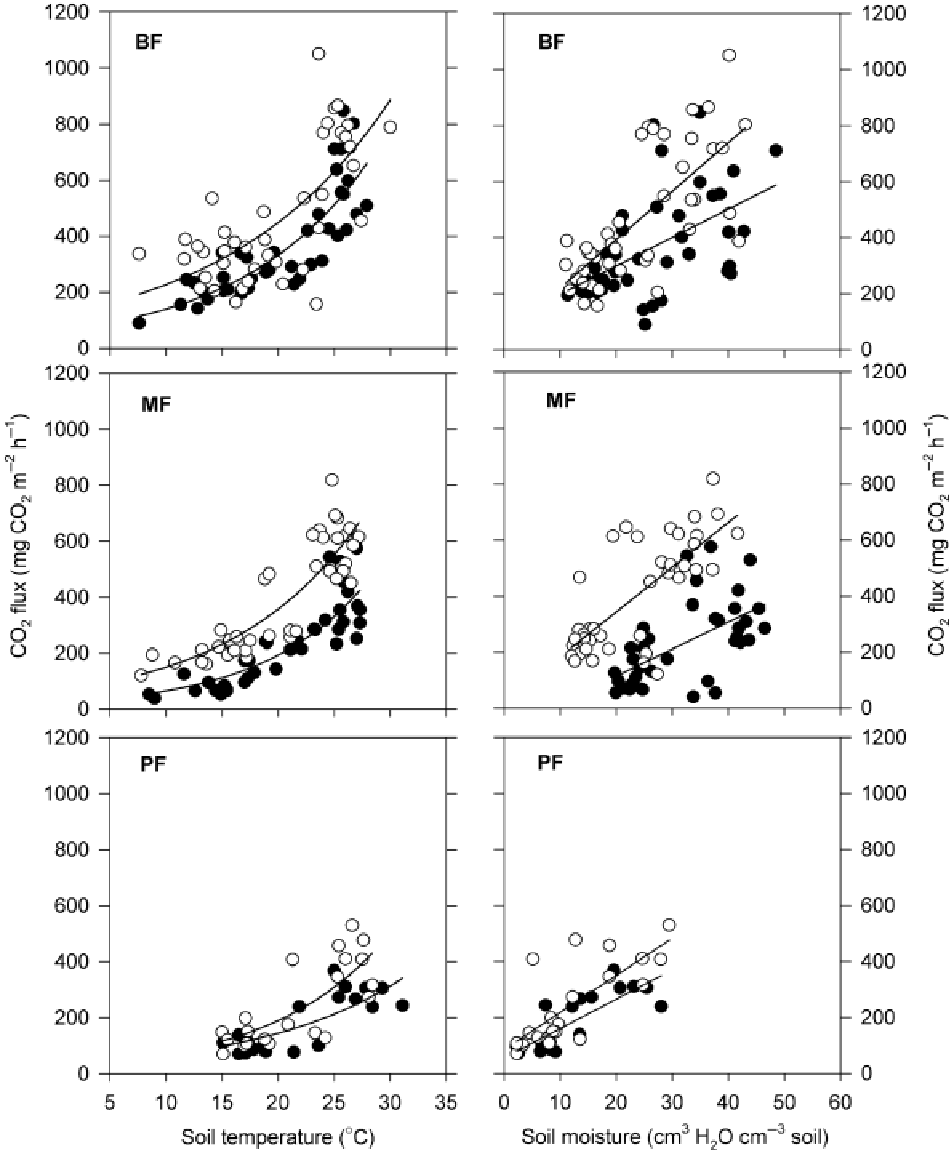

Fig. 4 Relationships between CO_2 fluxes and soil temperature at 5 cm below surface and volumetric soil moisture in the 0–5 cm soil layer in the pine (PF), mixed (MF), and broadleaf (BF) forest. Open and closed circles represent measurements from the control (SL) and the litter exclusion (BS) treatment, respectively. Coefficients of the regression lines are listed in Table 5.

the representativeness of the GHG fluxes presented in this paper at the regional scale cannot be evaluated. Many variables (e.g. forest age and topography) could be accentuating or dampening differences because of vegetation type. In order to quantify the impact of forest succession on GHG fluxes in the region, more sites should be investigated in the future.

Guangdong Province has experienced widespread afforestation in recent years because of economic growth. This type of afforestation is typical in south China and some other developing areas and results in an age structure dominated by young, pioneering forests. For example, pine forests accounted for 60% of total forested areas in Guangdong (Ren *et al*., 2002). If the observed increasing trend of GHG fluxes with forest successional progress in our study were representative at the regional scale, the strength of CH_4 sinks and N_2O sources may increase in the future in light of the natural succession of these young forests in southern China.

Effect of litter layer removal on soil-atmospheric GHG exchanges

Many studies indicate that litter removal reduces CO_2 emissions significantly (Dong *et al*., 1998; Rey *et al*.,

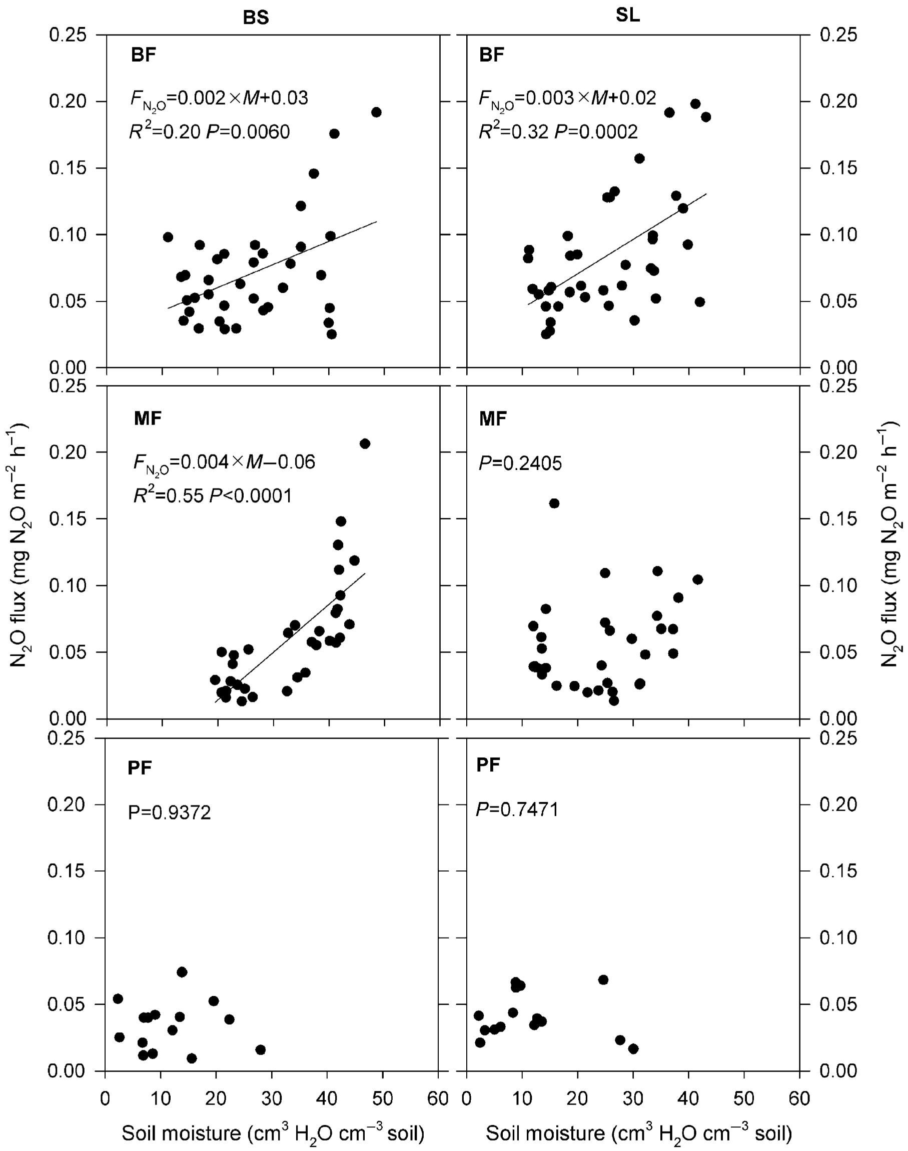

Fig. 5 Dependence of N_2O emission rates on soil moisture. Each datum is a mean value of three N_2O flux measurements and three soil water measurements at one site on a given day. Abbreviations are the same as in Fig. 2.

2002; Li *et al.*, 2004). Our results also demonstrated that litter removal reduced a considerable amount (29% on average) of CO_2 emission from the forest floor. The impact of litter exclusion is in general comparable with the mean value (20–30%) derived from forests worldwide by Raich & Nadelhoffer (1989). It is lower than values from a wet tropical forest in Puerto Rico (54–68%) (Li *et al.*, 2004), but higher than values from two temperate forests (i.e. 22% in deciduous forests in Germany (Dong *et al.*, 1998) and 21.9% in a Mediterranean mixed oak forest (Rey *et al.*, 2002)).

In contrast to CO_2 efflux, no distinct changes in CH_4 and N_2O fluxes were found after the litter layer was removed (Table 3). CH_4 and N_2O fluxes between soil and the atmosphere are largely determined by soil water content (Davidson *et al.*, 1993; Castro *et al.*, 1994, 2000; Bowden *et al.*, 1998; Kiese & Butterbach-Bahl, 2002). In this study, litter removal did not affect soil water content in most cases (Table 3), suggesting that minor changes in soil moisture were not sufficient to affect microbial activities. It also suggested that the majority of methane oxidation, nitrification, and denitrification activities happen in the mineral soil rather than in the surface litter in the DNR forests. This is consistent with Crill (1991) and Koschorrech & Conrad (1993) who found that the main CH_4-oxidizing activities were located in a zone at the top of mineral layer rather than in the organic layer.

Environmental dependency of soil-atmospheric GHG exchanges

A large body of literature considers soil temperature and water content as two of the most important environmental parameters controlling the temporal variation of soil CO_2 efflux for a given site (Lloyd & Taylor, 1994; Davidson *et al*., 1998, 2000; Buchmann, 2000; Fang & Moncrieff, 2001; Xu & Qi, 2001; Kiese & Butterbach-Bahl, 2002; Gough & Seiler, 2004). The model combined soil temperature and soil moisture (Table 5c) explained a considerable fraction of soil CO_2 variation, suggesting that both soil temperature and soil moisture are driving factors on soil CO_2 emission in the DNR. Studies in Mediterranean (Castro *et al*., 2000; Rey *et al*., 2002; Joffre *et al*., 2003) or semiarid ecosystems (Xu & Qi, 2001; Tang *et al*., 2004) also highlighted that soil CO_2 emission rates are controlled by both temperature and moisture. However, the way the two factors affect CO_2 efflux in those forests is quite different from that in our forests. Studies in these regions showed that soil temperature alone accounted for a major fraction of CO_2 emission variation when soil moisture was within a site-specific threshold value (Davidson *et al*., 1998; Xu & Qib, 2001; Rey *et al*., 2002). In our study, soil moisture showed a positive rather than negative relationship with temperature, as in the other studies (Fig. 4). This is partly caused by the fact that the soil moisture measurements were often lower than the field capacity of the soil (Table 1) and not high enough to reach the point when mineralization gets limited by reduced oxygen diffusion into the soil. Moreover, because of the covariation of soil moisture and temperature (Fig. 2b, c) driven by the simultaneous seasonal patterns of precipitation and air temperature, it is difficult, if not impossible, to distinguish the relative importance of moisture and temperature in controlling CO_2 emission rates.

Soil temperature did not have a strong effect on N_2O emissions. This is consistent with results reported in tropical, agricultural soils (Crill *et al*., 2000; Kiese & Butterbach-Bahl, 2002). Other field and laboratory studies (Garcia *et al*., 1991; Davidson *et al*., 1993; Kiese & Butterbach-Bahl, 2002) demonstrated that N_2O emissions were positively correlated with soil moisture content, which is in agreement with our study. However, the dependency of N_2O fluxes on soil moisture in our study was not as strong as that in other studies (Garcia *et al*., 1991; Davidson *et al*., 1993; Kiese & Butterbach-Bahl, 2002). In addition, the dependency of N_2O efflux on soil moisture was not observed in all forests, perhaps because low N availability in some of the plots with low N_2O fluxes was a more important limiting factor. N_2O fluxes were significantly positively correlated to soil moisture in the broadleaf forest and the bare soil in the mixed forest.

CH_4 fluxes did not display pronounced dependency on soil temperature, moisture, or their interaction, although higher CH_4 uptake rates were observed in the cool-dry season. This is different from similar studies in tropical and temperate forests, where CH_4 uptake rates were negatively related to soil moisture (Castro *et al*., 2000; Verchot *et al*., 2000). Soils change into CH_4 sources when soil moisture exceeds a site-specific value in those forests. Soil moistures throughout the study period were often lower than the water-holding field capacity. Soil moisture contents in our study sites probably did not reach the critical values needed to affect the activities of CH_4 consuming microbes during the study period.

The absence of strong statistical relationships between N_2O, CH_4, and soil water content is probably because of insufficient intensity of sampling. Verchot *et al*. (1999, 2000) showed N_2O and CH_4 emissions varied greatly in space, often requiring many chamber measurements to reliably estimate the mean flux of the site. Interestingly, they found the most spatially heterogeneous is CH_4, followed by N_2O and then CO_2, which agrees well with our findings on the correlations between GHG fluxes and soil water content: the poorest with CH_4, slightly better with N_2O, and the best with CO_2.

Conclusions

Soil CO_2 emissions within each of the forests were strongly correlated with soil temperature and soil moisture. Driven by seasonality of temperature and precipitation, soil CO_2 efflux showed a clear seasonal pattern, with fluxes significantly higher in the warm–humid season than in the cool-dry season. Although measurements of the CO_2, CH_4, and N_2O fluxes were taken simultaneously, CH_4 and N_2O fluxes were not strongly correlated with soil temperature and soil moisture, and no significant seasonal difference was detected in CH_4 and N_2O fluxes. These results probably suggest that factors other than soil moisture and temperature exerted a larger impact on CH_4 and N_2O fluxes than on CO_2 release and/or that there were not enough samples for CH_4 and N_2O flux measurements because of their higher spatial and temporal variability.

Forest succession strongly affects soil-atmospheric CO_2, CH_4, and N_2O fluxes, with the highest rates in the broadleaf forest, followed by the mixed forest and the pine forest. Enhanced GHG fluxes between soils and the atmosphere in later stages of forest succession suggest that the soil-atmospheric GHG fluxes in forests in southern China may increase in the future if the young forests that are currently dominant in the region become older, and if the observed trends from these forests are representative at the regional scale.

Soil surface litter removal resulted in a significant decrease in CO_2 emission, while it had no significant influence on CH_4 and N_2O fluxes. This suggests that the majority of the microbes related to CH_4 oxidization, nitrification, and denitrification exist in the mineral soil rather than in the surface litter layer.

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