SOIL HETEROTROPHIC RESPIRATION AND ACTIVE CARBON POOLS UNDER SUBTROPICAL FORESTS IN CHINA

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An understanding of the heterotrophic respiration part of belowground processes, as affected by active carbon, is crucial in order to predict the response of carbon emission from soil organic carbon, in forest ecosystems and climatic changes. However, in the current literature, most soil respiration measurements are interpreted without simultaneous information on active carbon pool dynamics. In this study, path analysis was used to demonstrate the impacts of microbial biomass carbon, water-soluble organic carbon and mineralisation carbon on soil heterotrophic respiration. It was found that variations in heterotrophic respiration were well related to mineralisation carbon and microbial biomass carbon, whereas water-soluble organic carbon was generally not adequate indicators of carbon effluxes. Mineralisation carbon and microbial biomass carbon have significant correlation relationships and indirect effects with each other on heterotrophic respiration, indicating a possible stimulatory effect of labile carbon and microbial activity on microbial processing of carbon. A single parameter recommended to quantify soil heterotrophic respiration in southern China is mineralisation carbon, as the most efficient measurement of soil variable.

Keywords: Microbial biomass carbon, water-soluble organic carbon, carbon mineralisation, subtropical forests

INTRODUCTION

Soil is a potentially important carbon sink, sequestering carbon from plants and soils (Bolin & Sukumar 2000). Conversely, soil can also be a carbon source, with microbes and other soil organisms releasing CO_2 to the atmosphere (Schlesinger & Andrews 2000). Soil organic matter and soil microorganisms determine whether soils act as sinks or sources of carbon in the global carbon cycle (Raich & Tufekcioglu 2000). Any dynamic changes in soil CO_2 emissions, in response to environmental changes and influence of global climate, identification of the factors that regulate the soil respiration is critical in predicting ecosystem responses to global change.

Soil CO_2 effluxes originate from different resources, including peat and litter decomposition (heterotrophic respiration), root respiration and respiration of organisms relying on root exudates. The temporal pattern of soil heterotrophic respiration was not only attributed to soil environment (Moyano et al. 2012), but also to soil organic substrates (Raich & Tufekcioglu 2000) and soil microorganisms (Tufekcioglu

et al. 2001). Soil organic matter encompasses various organic constitutes and fractions in soil, and it is notionally divided into three pools by distinct turnover rates: active, slow and passive (Figure 1) (Parton et al. 1987). Active carbon, although often a small fraction of soil organic carbon, significantly affects heterotrophic respiration at short timescales because of its rapid decomposition. Terminology such as microbial biomass carbon, water-soluble organic carbon, released carbon etc. are widely and often used to name active carbon pool in inconsistent ways (Rovira et al. 2010). So it is necessary to know which of these active carbon pools are significantly effective on soil heterotrophic respiration, and which act as non-significant.

The first aim of this research was to investigate the distribution of various soil carbon pools (total organic carbon, microbial biomass carbon, water-soluble organic carbon, mineralisation carbon) and soil heterotrophic respiration in different forests. It was hypothesised that, due to differences in forest stand and amount of organic matter, inputs will be distinguishable by
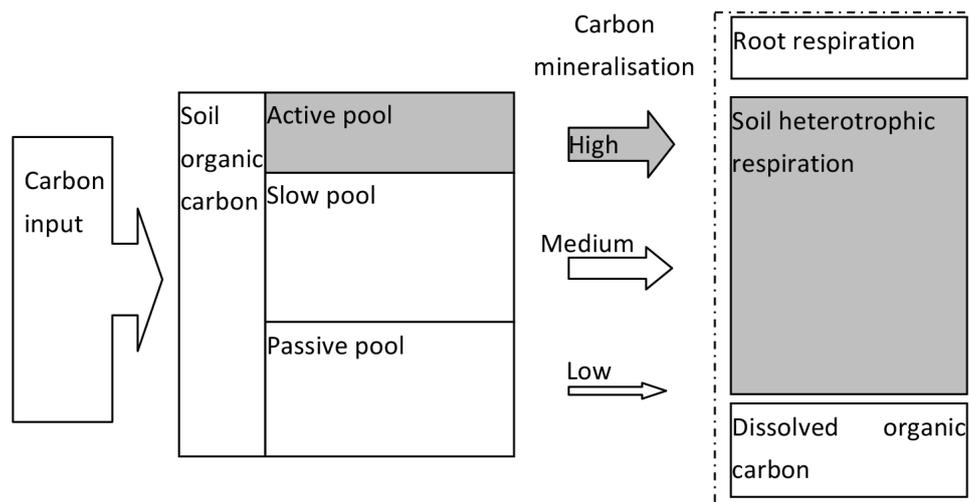
Figure 1   Simplified model on controls of soil organic carbon formation, mineralisation and heterotrophic respiration

their distribution of active carbon pools and soil heterotrophic respiration. A second objective was to assess the relationship between soil heterotrophic respiration and soil active carbon pools in forest ecosystem. It was assumed that the variation of soil heterotrophic respiration is the combined result of various soil active carbon, but not all are equally important. To understand its dynamics, it is necessary to know which of these active pools are more decisive, and which may act as a limiting factor for soil CO_2 effluxes.

MATERIALS AND METHODS

Study sites

The study sites were located at the Forest Ecological Research Station in Dagangshan (27° 30'–27° 50' N, 114° 30'–114° 45' E), Jiangxi Province, southern China, which has a typical humid subtropical climate with distinct rainy and dry seasons. The annual mean precipitation and air temperature are 1590 mm and 16.8 °C, respectively. Precipitation occurs mainly in summer (45%) (Wang et al. 2011). Three dominant tree species (*Pinus massoniana*, *Castanopsis fargesii* and *Phyllostachys pubescens*) were selected in this study.

At each site, three stands of different dominant species were established. The all dominant species were uneven-aged as it was impossible to find sites with stands of the same age. These stands were all under similar climate and soil properties, and therefore provided an ideal condition to study forest stand effect on soil carbon dynamics (Table 1). Soil was classified as Dystrochrept, according to U.S. Soil Taxonomy, 2nd edition.

Soil and stand properties

In March 2012 three 400 m² replicate plots were laid out in each forest stand of each site. Three 1 × 1 m subplots were randomly located in each plot. Five soil samples (0–10 cm) were randomly chosen in each subplot. Fifteen samples were collected in each forest stand. The wet-moist soil sample was sieved through a 2-mm mesh and divided into two parts. One was stored at 4 °C till the analysis for microbial biomass carbon and water-soluble organic carbon. The other part was air-dried for total organic carbon. Soils were also assessed for bulk density using a bulk density corer (diameter 5 cm).

On the external edges of the subplots, 60-cm deep trenches (below which few roots existed) were dug and lined with double-layer plastic sheets, then refilled with soil (Luan et al. 2011). Furthermore, all aboveground vegetation was carefully removed with minimal soil disturbance, and the trenched subplots were kept free of living vegetation throughout the study. At each trenched subplot, one PVC collar (19.6 cm inner diameter, 8 cm height) was installed to a depth of 5 cm for soil CO_2 efflux sampling (soil heterotrophic respiration). The first measurements were conducted after one week of collar establishment. All the PVC collars

Table 1   The main characteristics of the selected stands at soil sampling in this study

Forest stand	Soil pH	Soil bulk density (g cm^{-3})	Soil water content (%)	Clay (%)	Silt (%)	Sand (%)
Phyllostachys pubescens	4.79	0.92	25.9	8.81	45.24	45.91
Castanopsis fargesii	5.12	0.85	27.2	10.13	46.37	43.50
Pinus massoniana	4.86	1.10	26.5	9.02	41.31	49.67

were installed permanently throughout the observation campaigns.

Soil heterotrophic respiration (i.e., the total respiration rate excluding root respiration) was measured from April 2012 to March 2013 using a Li-8100 soil CO_2 flux system. All measurements were taken twice per month, every 2 hours during the day and every 3 hours during the night (Wang et al. 2011). To minimise measurement errors and equipment damage, all measurements were taken on sunny days without precipitation and/or high winds. Soil temperature was measured simultaneously with respiration at a depth of 5 cm in the vicinity of the collars with a portable temperature probe provided with Li-8100.

Microbial biomass carbon was analysed by chloroform fumigation extraction method (Vance et al. 1987). First, 25 g fresh soil was fumigated with chloroform for 24 h, and then extracted with 0.5 M K_2SO_4 for 2 h on a shaker. The extracts were centrifuged and filtered (Whatman 42). Similar sets of non-fumigated sample were extracted the same way. Carbon concentration in the extracted solutions was measured by a TOC analyser. Microbial biomass carbon concentration was determined following the method of Wu et al. (1990):

$$MBC = (F - C) / K_c \qquad (1)$$

where MBC = microbial biomass carbon, F and C = carbon concentrations in the extracts of fumigated and non-fumigated soils respectively, and $K_c = 0.45$, which is the proportionality factor to convert (F − C) to MBC.

Water-soluble organic carbon was extracted from 30 g of fresh soil with an addition of 60 ml of distilled water (Xu et al. 2010). The mixture was shaken for 30 min on a shaker (250 rpm) at 20 °C, centrifuged for 20 min at 3500 rpm and the supernatant liquid was filtered through 0.45 μm cellulose nitrate membrane filter. Water-soluble organic carbon in extracts was measured by a TOC analyzer.

Total organic carbon was digested in $K_2Cr_2O_7$-H_2SO_4 solution using oil-bath heating at 155 °C (Ministry of Forestry 2000). The soil texture and water content were analysed by the pipette method (Lu 2011). Soil pH was measured on a soil water suspension (1 : 2.5 water suspension). Soil carbon mineralisation was estimated by using the incubation method described by De Neve and Hofman (2000). Soil samples (100 g) of each treatment, preconditioned at 75% of water holding capacity, were placed in 1 L stoppered glass jars and tightly sealed and incubated at 25 °C. Meanwhile, controls (without soil samples) were also incubated in the incubators. Small vials (50 ml, with no lids) containing 30 ml of 1 mol L^{-1} NaOH solution were periodically placed in each jar to trap carbon dioxide evolved from the soil. Samples were taken after 1, 4, 6, 11, 13, 25, 35, 46, 56, 67, 77, 88 and 98 days by removing the NaOH vials. The amount of CO_2 was determined by titration with 1 mol L^{-1} HCl to pH 8.3 in the presence of 1 mol L^{-1} BaCl$_2$. The functional carbon pool sizes and their turnover rates were determined, following a double exponential equation model (Rovira et al. 2010):

$$C_{TM}(t) = C_{LM}(1 - e^{-k_{LM}t} + C_{PM}(1 - e^{-k_{PM}t}) \qquad (2)$$

where $C_{TM}(t)$ = total cumulative mineralised carbon at time t (in days), C_{LM} = labile mineralisable carbon, C_{PM} = potentially mineralisable carbon, k_{LM} = mineralisation rate of labile mineralisable carbon and k_{PM} = potentially mineralisable carbon.

Statistical analyses

In addition to Pearson linear correlation and ANOVA analysis, the relationship among the parameters was studied by path analysis, using Sigmastat package. Path analysis is a multivariate statistical technique developed by the geneticist Wright (1921). It was developed

as a method of decomposing correlations into different pieces for interpretation of effects, enabling people to lucubrate the causal relationship between cause variables and outcome variables through related surface phenomena, so as to provide a reliable basis for statistical decision.

A simple diagram will illustrate the basic ideas of path analysis. Suppose there are three variables, x, y and z, showing a causal relationship between them, simply, x and y is the cause of z, and there is a correlation between x and y. To satisfy the requirement of causal closure, all other unknown factors causally connected with z are subsumed by residual variable (e_y). Path diagram with coefficients is shown in Figure 2 (Wright 1934 & Li et al. 2011).
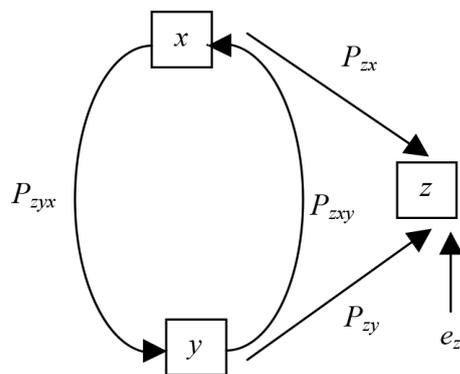
Figure 2　Path diagram with coefficients

Using path analysis, it was evaluated whether other soil variables (e.g., total organic carbon, microbial biomass carbon, water-soluble organic carbon or cumulative mineralisation carbon) explained significant variation in values of soil heterotrophic respiration. Based on multiple lineal regression analysis, path coefficients were calculated according to Li et al. (2011). Correlation coefficients were divided into: 1) the direct influence of the independent variable (total organic carbon, microbial biomass carbon, water-soluble organic carbon or cumulative mineralisation carbon) on the dependent variable (soil heterotrophic respiration) and 2) the indirect influence of one independent variable through another independent variable on the dependent variable.

RESULTS

Soil organic carbon pools

Total organic carbon differed significantly among tree species, with *C. fargesii* > *P. pubescens* > *P. massoniana* (Table 2). On average, microbial biomass carbon in the 0–10 cm soil layer represented 1–3% of total organic carbon. Water-soluble organic carbon was less than 1% of total organic carbon. Therefore, microbial biomass carbon represented a greater portion of total organic carbon than water-soluble organic carbon. Microbial biomass carbon and water-soluble organic carbon beneath *C. fargesii* were significantly greater than beneath *P. pubescens* and *P. massoniana*. MBC/TOC was highest beneath *C. fargesii*, while WSOC/TOC in *P. pubescens* was highest.

Soil organic carbon mineralisation

The cumulative mineralisation carbon ranged from 1.21 to 4.02 g kg^{-1}. The cumulative mineralisation carbon was high in the *C. fargesii* soil (Table 2), and the conversion of *C. fargesii* into *P. pubescens* and *P. massoniana* resulted in a significant decrease of cumulative mineralisation carbon. The cumulative mineralisation carbon in *P. pubescens* was higher than that in *P. massoniana*. The values of labile mineralisable carbon ranged from 0.25 g kg^{-1} to 0.64 g kg^{-1} in three forests. The C_{LM} showed a significant decrease of 60% because of the conversion into *P. pubescens,* and 30 % was ascribed to the conversion into *P. massoniana* (Table 3). The potentially mineralisable carbon ranged from 1.41 g kg^{-1} to 6.23 g kg^{-1}, highest in *C. fargesii*, moderate in *P. pubescens* and lowest in *P. massoniana.*

With increasing incubation time, a decline in cumulative mineralisation carbon was observed in the study (Figure 3). In general, carbon mineralisation followed a similar pattern for all soil samples, which was fast during the first 15 days and slowed down in the next 90 days. The C_{LM} rate ranged from 0.90 to 2.89 g kg^{-1} soil d^{-1} and was significantly higher in *P. pubescens* soil than that from other forest stands (Table 3). Furthermore, the C_{LM} rate from *P. massoniana* soil decreased compared with that of *C. fargesii* soil. The C_{PM} rate was much lower than C_{LM} rate, ranging from 0.0009 to 0.011 mg kg^{-1} soil d^{-1}, and ranked as *P. massoniana* > *C. fargesii* > *P. pubescens*.

Table 2   Mean soil carbon pools, mineralisation and soil heterotrophic respiration rates in three forests

Forest stand	TOC (g kg^{-1})	MBC (g kg^{-1})	WSOC (g kg^{-1})	HR (g m^{-2} d^{-1})	C_{TM} (g kg^{-1})	C_{TM} rate (g kg^{-1} d^{-1})
Pinus massoniana	27.72 ± 1.22c	0.44 ± 0.09c	0.07 ± 0.02b	0.37 ± 0.12c	1.21 ± 0.08c	0.01 ± 0.00b
Phyllostachys pubescens	36.45 ± 3.14b	0.72 ± 0.10b	0.14 ± 0.03a	0.58 ± 0.12b	1.83 ± 0.18b	0.02 ± 0.00b
Castanopsis fargesii	40.78 ± 1.82a	1.02 ± 0.30a	0.11 ± 0.04a	1.34 ± 0.12a	4.02 ± 0.31a	0.04 ± 0.01a

Column values are mean ± SE; similar letters are not significantly different at p < 0.05; TOC = total organic carbon, MBC = microbial biomass carbon, WSOC = water-soluble organic carbon, HR = soil heterotrophic respiration and C_{TM} = cumulative mineralisation carbon

Table 3   Contribution of the labile mineralisable carbon and potentially mineralisable carbon over the course of incubation

Forest stand	C_{LM} (g kg^{-1})	k_{LM} (g kg^{-1} d^{-1})	C_{PM} (g kg^{-1})	k_{PM} (g kg^{-1} d^{-1})
Pinus massoniana	0.25 ± 0.03c	1.81 ± 0.0.02b	1.41 ± 0.01c	0.011 ± 0.01a
Phyllostachys pubescens	0.46 ± 0.01b	2.89 ± 0.10a	3.16 ± 0.04b	0.001 ± 0.00c
Castanopsis fargesii	0.62 ± 0.05a	0.90 ± 0.07c	6.23 ± 0.11a	0.005 ± 0.00b

C_{LM} = labile mineralisable carbon, C_{PM} = potentially mineralisable carbon, k_{LM} = mineralisation rate of labile mineralisable carbon and k_{PM} = mineralisation rate of potentially mineralisable carbon
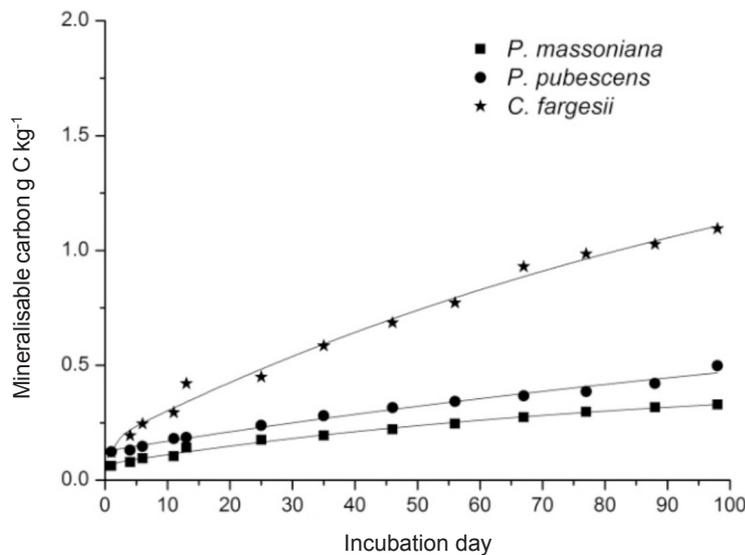
Figure 3   Dynamics of carbon mineralisation during the incubation

Soil heterotrophic respiration

The seasonal pattern of soil heterotrophic respiration was similar to soil temperature. It was found that the mean soil heterotrophic respiration in forests was 1.06 g C m^{-2} d^{-1} in the growing season and 0.47 g C m^{-2} d^{-1} in the non-growing season. The annual maximum and minimum soil heterotrophic respiration were 2.67 and 0.19 g C m^{-2} d^{-1} respectively, with the maximum occurring in July and August and the minimum in January and February (Figure 4). In the three forests, the mean values of soil heterotrophic respiration ranged from 0.37 to 1.34 g C m^{-2} d^{-1}. The mean heterotrophic respiration in *C. fargesii* was significantly higher than in *P. pubescens* and *P. massoniana* (Table 2).
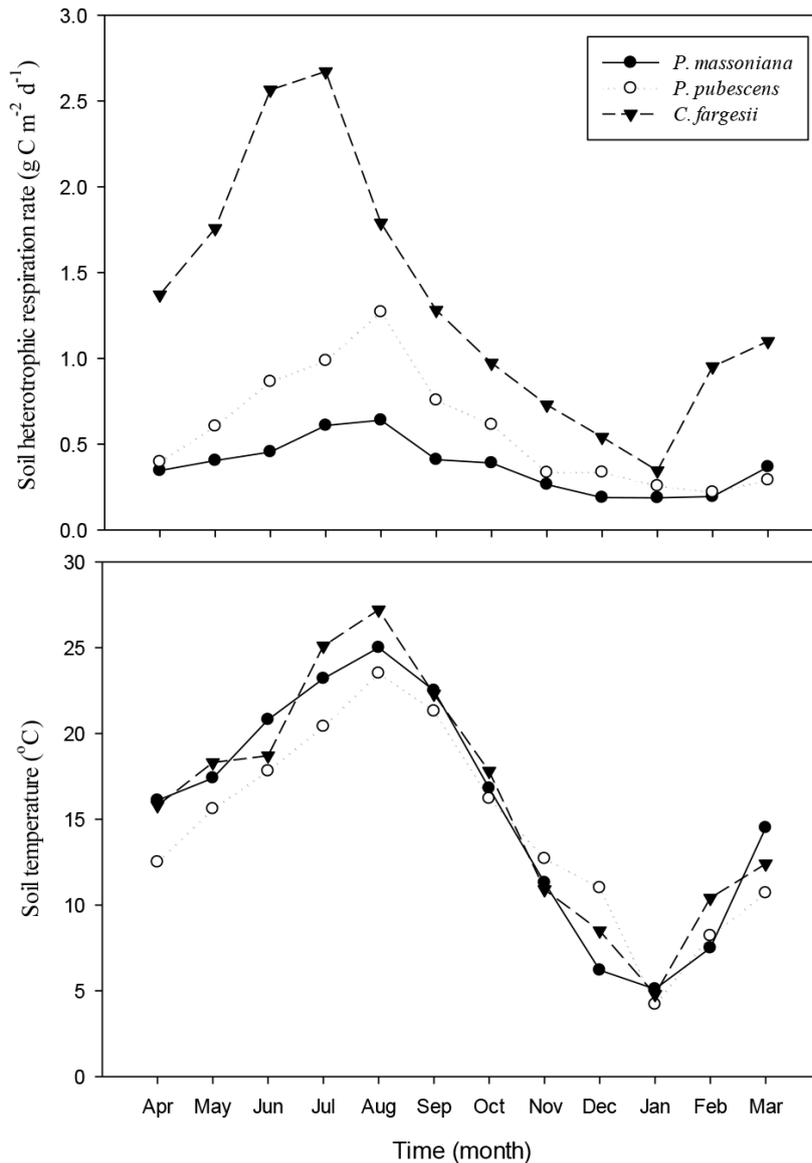
Figure 4   Seasonal patterns of soil heterotrophic respiration rates and soil temperature in the three forests during 2012–2013

Soil carbon pools and soil heterotrophic respiration relationships

Relationships between soil heterotrophic respiration and soil carbon pools such as total organic carbon, microbial biomass carbon, water-soluble organic carbon and cumulative mineralisation carbon were examined using linear correlation technique. The strength of these relationships across all soils of this study was indicated by Pearson correlation (Table 4). The strongest correlation relationship with soil heterotrophic respiration was found with cumulative mineralisation carbon (r = 0.806, 0.905, 0.928). The soil heterotrophic respiration

showed a stronger correlation relationship with microbial biomass carbon (r = 0.761, 0.801, 0.923) than with total organic carbon, though some relationships were significant. The HR-WSOC relationship was weak and not significant. This signifies that it is necessary to carry out the path analysis, as indirect influences on soil heterotrophic respiration is relevant.

The path model had the highest explanatory power, with adjusted R^2 values of 0.943, 0.780 and 0.939. Cumulative mineralisation carbon was the strongest positive direct effect (0.659, 0.444, 0.582) on soil heterotrophic respiration, followed by microbial biomass carbon (0.328, 0.383, 0.310) (Table 5). The relatively high

Table 4   Correlation coefficients between carbon pools and soil heterotrophic respiration in three forests

Forest stand	Fraction	HR	TOC	MBC	WSOC	$_c$TM
Pinus massoniana	TOC	0.432	_	0.154	0.481	0.340
	MBC	0.801**	0.154	_	0.020	0.676
	WSOC	0.200*	0.481	0.020	_	0.256
	C_{TM}	0.928**	0.340	0.676	0.256	_
Phyllostachys pubescens	TOC	0.721*	_	0.786**	0.503	0.729*
	MBC	0.761*	0.786**	_	0.441	0.709
	WSOC	0.143	0.503	0.441	_	0.294
	C_{TM}	0.806**	0.729*	0.709	0.294	_
Castanopsis fargesii	TOC	0.615	_	0.554	-0.069	0.478
	MBC	0.923**	0.554	_	0.178	0.838**
	WSOC	0.119	-0.069	0.178	_	-0.135
	C_{TM}	0.905**	0.478	0.838**	-0.135	_

*Significant at p < 0.05, ** significant at p < 0.01; HR = soil heterotrophic respiration, TOC = total organic carbon, MBC = microbial biomass carbon, WSOC = water-soluble organic carbon and C_{TM} = cumulative mineralisation carbon

Table 5   Path coefficients of the effects of carbon fractions and microbial activity on soil heterotrophic respiration in forests

Forest stand	Variables	Direct path coefficient	Indirect path coefficient			
			TOC	MBC	WSOC	C_{TM}
Pinus massoniana	TOC	0.188	_	0.051	-0.031	0.224
	MBC	0.328	0.029	_	-0.010	0.222
	WSOC	-0.065	0.090	0.007	_	0.169
	$_c$TM	0.659	0.064	0.222	-0.022	_
Phyllostachys pubescens	TOC	0.235	_	0.349	-0.138	0.279
	MBC	0.383	0.185	_	-0.216	0.315
	WSOC	-0.275	0.118	0.196	_	0.113
	C_{TM}	0.444	0.171	0.315	-0.200	_
Castanopsis fargesii	TOC	0.176	_	0.172	-0.011	0.278
	MBC	0.310	0.098	_	0.086	0.260
	WSOC	0.155	-0.012	0.055	_	-0.079
	C_{TM}	0.582	0.084	0.074	0.260	_

TOC = total organic carbon, MBC = microbial biomass carbon, WSOC = water-soluble organic carbon and C_{TM} = cumulative mineralisation carbon

positive indirect effects on soil heterotrophic respiration were also caused by cumulative mineralisation carbon and microbial biomass carbon. In contrast, water-soluble organic carbon had a negative direct effect on soil heterotrophic respiration in *P. pubescens* and *P. massoniana*, whereas the indirect effects of water-soluble organic carbon through other characteristics were positive and higher than direct effect. Its low correlation coefficient with soil heterotrophic respiration was mainly caused by its negative direct effect. But the water-soluble organic carbon from *C. fargesii* soil was positive direct effect on soil heterotrophic respiration. Total organic carbon showed the least positive direct effect (0.176, 0.188, 0.235) on soil heterotrophic respiration, while it had high indirect effect through cumulative

mineralisation carbon and microbial biomass carbon, resulting in medium positive correlation with soil heterotrophic respiration.

DISCUSSION

Active carbon pool

Correlation of soil heterotrophic respiration with cumulative mineralisation carbon was better than the one obtained with microbial biomass carbon or water-soluble organic carbon. Rovira et al. (2010) also found that water-soluble organic carbon did not significantly correlate with basal respiration, and observed that the relationship with microbial biomass carbon was much stronger. Water-soluble organic carbon with active carbon pool was less adequate, owing to the poor direct effect obtained between water-soluble organic carbon and soil heterotrophic respiration in this study. Indirect effects on soil heterotrophic respiration through microbial biomass carbon and cumulative mineralisation carbon is higher than that of direct effect, and a significant correlation between water-soluble carbon and soil microbial activity has been observed. Hagedorn et al. (2004) observed that soluble carbon of forest soils is mainly derived from medium-aged to old organic matter, stabilised in the fine fractions. Wagai and Sollins (2002) also found that water-soluble organic carbon biodegradation is neither easy nor fast. At any rate, water-soluble organic carbon is much smaller than microbial biomass carbon Thus, cumulative mineralisation carbon is considered a good estimator of active carbon, in response to forest changes. Since the amount of cumulative mineralisation carbon is much higher than that of water-soluble organic carbon and microbial biomass carbon, cumulative mineralisation carbon should account for most of the active carbon.

Comparisons of soil heterotrophic respiration

The factors contributing within-ecosystem soil respiration variability are complex because soil CO_2 flux is composed of several different components (Hanson et al. 2000). The variation and controlling mechanisms of different components were different among stands (Luan et al. 2011). The variation in soil heterotrophic respiration is mainly controlled by the soil biophysical environment and substrate availability,

such as aboveground and belowground litter (Ryan & Law 2005), soil organic carbon (Xu & Qi 2001) or labile organic carbon (Laik et al. 2009). Similar to Wang and Yang (2007), it was found that forest stand effects soil heterotrophic respiration.

In this study, *C. fargesii* had higher soil heterotrophic respiration per month compared to other forests (Figure 3), and this led to a significantly higher mean soil heterotrophic respiration (Table 2). However, higher soil temperature was not observed in *C. fargesii,* compared to the other forests (p > 0.05). Therefore, the higher RH in this forest may be accounted for by higher cumulative mineralisation carbon and soil organic carbon, rather than temperature. Various soil carbon pools, especially the cumulative mineralisation carbon, in the topsoil, explained the pattern of soil heterotrophic respiration across the three forests (Table 5). The results were also consistent with Xu and Qi's (2001) who found that soil heterotrophic respiration in ponderosa pine (*Pinus ponderosa*) plantation in California was significantly and positively correlated with soil organic matter content. Furthermore, a higher correlation and path coefficients were found in cumulative mineralisation carbon versus soil heterotrophic respiration, microbial biomass carbon vs. soil heterotrophic respiration, total organic carbon vs. HR and water-soluble organic carbon vs. soil heterotrophic respiration. This indicated the higher contribution of cumulative mineralisation carbon and microbial biomass carbon to soil respiration. This further illustrated that the variations in soil heterotrophic respiration across forests can be mainly attributed to different cumulative mineralisation carbon (Raich & Tufekcioglu 2000) and substrate (microbial biomass carbon) availability (Wang et al. 2010). Thus, cumulative mineralisation carbon is considered a good indicator of soil organic matter quality (Saviozzi et al. 2002). Soil microbial biomass can be also used as a potential early, sensitive indicator of soil organic carbon changes (Huang & Song 2010).

Comparisons of carbon pools in different forest stand

Forest stand had a positive influence on total soil organic carbon (Table 2), which was also observed by Ruiz-Jaen and Potvin (2010). The total organic carbon content depends on the balance

between carbon input and carbon effluxes. Since most carbon is returned to the soil through litter, litter production and decomposition rates are estimated to predict carbon input from vegetation to soil (Zhang & Wang, 2012). Litter decomposition rate is influenced by tree characteristics such as C : N ratio and leaf quality, which in turn were dependent on tree species. The results showed that *C. fargesii* had higher total organic carbon than *P. pubescens* and *P. massoniana*. These differences could be attributed to chemical and physical differences in the litter of coniferous versus broadleaf forests, the former containing more components that are difficult to decompose, which results in litter accumulation on the forest floor and less carbon incorporation into the mineral soil (Wang et al. 2009).

In this study, forest stands affected not only total organic carbon content but also carbon fractions, as shown by Yang et al. (2009). Higher microbial biomass carbon and water-soluble organic carbon appeared in *C. fargesii* compared with *P. pubescens* and *P. massoniana*. This result is similar with other studies. Smolander and Kitunen (2002) found that broadleaved forest contained higher microbial biomass carbon and water-soluble organic carbon than coniferous forest. Mineralisable carbon is the key component of soil organic carbon circulation (Nsabimana et al. 2004; Shi et al. 2009). In this study, forest stand significantly affected soil carbon mineralisation, and *C. fargesii* soil had higher cumulative mineralisation carbon and cumulative mineralisation carbon rate than *P. pubescens* and *P. massoniana* soils. The low quality (or quantity) of soil organic carbon limits the source of energy required for soil microbial growth, which eventually decreases the cumulative mineralisation carbon rate. Zhang et al. (2009) reported that increased soil labile carbon pools and soil microbial biomass could improve soil carbon mineralisation. The soil heterotrophic respiration in *P. pubescens* and *P. massoniana* soils also illustrated decreased soil organic carbon consumption compared with *C. fargesii* soil.

More importantly, laboratory incubation measurements in carbon mineralisation can be used to estimate the pool sizes of hypothetical fractions of soil organic matter and the turnover rates of these pools (Bonde & Rosswall 1987). In this study, double exponential equation model were used to estimate two pools of labile mineralisable carbon and potentially mineralisable carbon. The estimated value of C_{LM}/TOC was similar to that reported from subtropical forest soils (1.04–1.70%) (Zhang et al. 2009). However the C_{LM}/TOC was lower than the temperate forest of Northeast China, which may be due to the relatively high organic matter content and low decomposition rate in temperate forest soils (Burton et al. 2010).

CONCLUSIONS

In conclusion, soil surface CO_2 fluxes from soil heterotrophic respiration, varying with forest stands, are mainly controlled by cumulative mineralisation carbon and microbial biomass carbon. Cumulative mineralisation carbon is a good indicator for predicting temporal and spatial variations of heterotrophic respiration. It is recommended that if a single carbon fraction measurement must be chosen to reflect the heterogeneity of soil heterotrophic respiration rate in forest soils, cumulative mineralisation carbon, rather than total organic carbon or other active carbon (microbial biomass carbon or water-soluble organic carbon), is the most efficient.

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REFERENCES

BOLIN B & SUKUMAR R. 2000. Global perspective: land use, change, and forestry. Pp 23–51 in Watson RT, Noble IR, Bolin B, Ravindranath NH, Verardo DJ & Dokken DJ (eds) *A Special Report of the IPCC*, Cambridge University Press, Cambridge.

BONDE TA & ROSSWALL T. 1987. Seasonal variation of potentially mineralisable nitrogen in four cropping systems. *Soil Science Society of America Journal* 51: 1508–1514.

BURTON J, CHEN CR, XU ZH & GHADIRI H. 2010. Soil microbial biomass, activity and community composition in adjacent native and plantation forests of subtropical Australia. *Journal of Soils and Sediments* 10: 1267–1277.

DE NEVE S & HOFMAN G. 2000. Influence of soil compaction on carbon and nitrogen mineralization of soil organic matter and crop residues. *Biology and Fertility of Soil* 30: 544–549.

Hagedorn F, Saurier M & Blaser P. 2004. A 13C tracer study to identify the origin of dissolved organic carbon in forested mineral soils. *Eeuropean Journal of Soil Science* 55: 91–100.

Hanson PJ, Edwards NT, Garten CT& Andrews JA. 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry* 48: 115–146.

Huang J & Song C. 2010 Effects of land use on soil water soluble organic C and microbial biomass C concentrations in the Sanjiang Plain in Northeast China. Acta Agriculturae Scandinavica, Section B. *Soil and Plant Science* 60: 182–188.

Laik R, Kumar K, Das DK & Chaturvedi OP. 2009. Labile soil organic matter pools in a calciorthent after 18 years of afforestation by different plantations. *Applied Soil Ecology* 42: 71–78.

Li HN, Mu HL, Zhang M & Li N. 2011. Analysis on influence factors of China´s CO_2 emissions based on Path-STIRPAT model. *Energy Policy* 39: 6906–6911.

Lu RK. 2011. Methods of Soil Agricultural Chemistry Analysis. Chinese Agricultural Science and Technology Press, Beijing.

Luan JW, Liu SR, Wang JX, Zhu XL & Shi ZM. 2011. Rhizospheric and heterotrophic respiration of a warm-temperate oak chronosequence in China. *Soil Biology & Biochemistry* 43: 503–512.

Ministry of Forestry. 2000. *Forest Soil Analysis Methods.* Chinese Criteria Press, Beijing.

Moyano FE, Vasilyeva N, Bouckaert L et al. 2012. The moisture response of soil heterotrophic respiration: interaction with soil properties. *Biogeosciences* 9: 1173–1182.

Nsabimana D, Haynes RJ & Wallis FM. 2004. Size, activity and catabolic diversity of the soil microbial biomass as affected by land use. *Applied Soil Ecology* 26: 81–92.

Parton WJ, Schimel DS, Cole CV & Ojima DS. 1987. Analysis of the factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal* 51: 1173–1179.

Raich JW & Tufekcioglu A. 2000. Vegetation and soil respiration: correlations and controls. *Biogeochemistry* 48: 71–90.

Rovira P, Jorba M & Romanyà J. 2010. Active and passive organic matter fractions in Mediterranean forest soils. *Biology and Fertility of Soil* 46: 355–369.

Ruiz-Jaen MC & Potvin C. 2010. Tree diversity explains variation in ecosystem function in a Neotropical forest in Panama. *Biotropica* 42: 638–646.

Ryan MG & Law BE. 2005. Interpreting, measuring, and modeling soil respiration. *Biogeochemistry* 73: 3–27.

Saviozzi A, Bufalino P, Levi-minizi R & Riffaldi R. 2002. Biochemical activities in a degraded soil restored by two amendments: a laboratory study. *Biology and Fertility of Soil* 35: 96–101.

Schlesinger WH & Andrews JA. 2000. Soil respiration and the global carbon cycle. *Biogeochemistry* 48: 7–20.

Shi Z, Li YP, Wang SJ et al. 2009. Accelerated soil CO_2 efflux after conversion from secondary oak forest to pine plantation in southeastern China. Ecological Research 24: 1257–1265.

Smolander A & Kitunen V. 2002. Soil microbial activities and characteristics of dissolved organic C and N in relation to tree species. *Soil Biology & Biochemistry* 34: 651–660.

Tufekcioglu A, Raich JW, Isenhart TM & Schultz RC. 2001. Soil respiration within riparian buffers and adjacent crop fields. *Plant and Soil* 229: 117–124.

Vance ED, Brookes PC & Jenkinson DS. 1987. An extraction method for measuring soil microbial biomass-C. *Soil Biology & Biochemistry* 19: 703–707.

Wagai R & Sollins P. 2002. Biodegradation and regeneration of water-soluble carbon in a forest soil: leaching column study. *Biology and Fertility of Soil* 35: 18–26.

Wang B, Jiang Y, Wei XH, Zhao GD, Guo H & Bai XL. 2011. Effects of forest stand, stand age, and altitude on soil respiration in subtropical forests of China. *Scandinavian Journal of Forest Research* 26: 40–47.

Wang QK, Wang SL & Zhang JW. 2009. Assessing the effects of vegetation types on carbon storage fifteen years after reforestation on a Chinese fir site. *Forest Ecology and Management* 258: 1437–1441.

Wang SL, Zhang WD & Sanchez F. 2010. Relating net primary productivity to soil organic matter decomposition rates in pure and mixed Chinese fir plantations. *Plant and Soil* 334: 501–510.

Wang C & Yang J. 2007. Rhizospheric and heterotrophic components of soil respiration in six Chinese temperate forests. *Global Change Biology* 13: 123–131.

Wang W, Peng S, Wang& T & Fang J. 2010. Winter soil CO_2 efflux and its contribution to annual soil respiration in different ecosystems of a forest-steppe ecotone, north China. *Soil Biology & Biochemistry* 42: 451–458.

Wright S. 1921. Correlation and causation. *Journal of Agricultural Reaearch* 20: 557–585.

Wright S. 1934. The method of path coefficients. *Annals of Mathematiacal Statistics* 5: 161–215.

Wu J, Joergensen RG, Pommerening B, Chaussod R & Brookes PC. 1990. Measurement of soil microbial biomass C by fumigation–extraction: an automated procedure. *Soil Biology & Biochemistry* 22: 1167–1169.

Xu M & Qi, Y. 2001. Soil-surface CO_2 efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California. *Global Change Biology* 7: 667–677.

Xu X, Zhou Y, Ruan HH, Luo YQ & Wang JS. 2010. Temperature sensitivity increases with soil organic carbon recalcitrance along an elevational gradient in the Wuyi Mountains, China. *Soil Biology & Biochemistry* 42: 1811–1815.

Yang YS, Guo JF, Chen GS, YinYF, Gao R & Lin CF. 2009. Effects of forest conversion on soil labile organic carbon fractions and aggregate stability in subtropical China. *Plant and Soil* 323: 153–162.

Zhang J, Wang SL & Feng ZW. 2009. Carbon mineralization of soils from native evergreen broadleaf forest and three plantations in mid-subtropic China. *Communications in Soil Science and Plant Analysis* 40: 1964–1982.

Zhang WD & Wang SL. 2012, Effects of NH_4^+ and NO_3^- on litter and soil organic carbon decomposition in a Chinese fir plantation forest in South China. *Soil Biology & Biochemistry* 47: 116–122.