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Are variations in heterotrophic soil respiration related to changes in substrate availability and microbial biomass carbon in the subtropical forests?

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Soil temperature and moisture are widely-recognized controlling factors on heterotrophic soil respiration (R_h), although they often explain only a portion of R_h variability. How other soil physicochemical and microbial properties may contribute to R_h variability has been less studied. We conducted field measurements on R_h half-monthly and associated soil properties monthly for two years in four subtropical forests of southern China to assess influences of carbon availability and microbial properties on R_h . R_h in coniferous forest was significantly lower than that in the other three broadleaf species-dominated forests and exhibited obvious seasonal variations in the four forests ($P < 0.05$). Temperature was the primary factor influencing the seasonal variability of R_h while moisture was not in these humid subtropical forests. The quantity and decomposability of dissolved organic carbon (DOC) were significantly important to R_h variations, but the effect of DOC content on R_h was confounded with temperature, as revealed by partial mantel test. Microbial biomass carbon (MBC) was significantly related to R_h variations across forests during the warm season ($P = 0.043$). Our results suggest that DOC and MBC may be important when predicting R_h under some conditions, and highlight the complexity by mutual effects of them with environmental factors on R_h variations.

With about 68–79 petagram (Pg) CO_2 -C being released into the atmosphere each year, soil respiration is the second largest carbon (C) flux in the terrestrial C cycling^{1,2}. Because variations in soil respiration are most likely to upset the equilibrium of terrestrial C cycling^{3,4}, soil respiration has received increasing concerns in recent decades⁵. Total soil respiration (R_s) consists of two components, i.e., autotrophic (R_a) and heterotrophic (R_h) respiration, with R_a mainly being the CO_2 released by plant roots and R_h by microbial activities in association with soil organic matter (SOM) decomposition^{6,7}. Averaged on the global scale, R_h accounts for 54% of R_s in forests⁶. Temperature and water supply, interactively or separately, have been most frequently reported to control soil respiration^{1,8,9}, and account for a certain portion of variations in soil respiration in previous studies^{5,8,10}. However, which factors contribute to the remaining proportion is still an active topic.

Substrate availability is proposed as an important underlying factor influencing soil respiration^{5,11}, and even overshadows the role of temperature in the processes of soil respiration in specific ecosystems^{12,13}. A positive substrate- R_h relationship has been found under laboratory conditions, especially when soil microbes are energy-limited¹⁴. The increase in CO_2 efflux rate with C additions may be attributed to reactivations of dormant microorganisms¹⁵, augments in microbial biomass and activity^{14,16}, and shifts in microbial community composition and growth strategies¹⁷. Substrate-dependent soil respiration was also noted in field studies^{12,18}, but this

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was often based on statistically significant relationships between soil respiration rate and primary productivity¹², photosynthates¹⁸, or litter production¹⁹. Caution should be taken when one would extend to a conclusion that substrate availability significantly influences R_h , because soil substrate content is not always significantly related to vegetation productivity²⁰. Few studies have related periodically-measured R_h to the according soil substrate content in fields, as did in the study of Iqbal *et al.*²¹.

In natural ecosystems, soil organic C constitutes of various C-contained compounds. In spite of being analysed by means of diverse extraction/assay procedures in different studies, SOC can be pooled as labile and recalcitrant SOC, or in some cases named as fast and slow turnover C pools etc.²². Labile (or fast turnover) SOC fractions can be easily utilized while recalcitrant (or slow turnover) C compounds are often hardly-decomposed by soil microorganisms¹⁷. Consequently, differences in the content of these SOC fractions may result in differed soil respiration, especially heterotrophic respiration, due to the nature of decomposability and preference by soil microorganisms. Labile SOC content, e.g., represented by the concentration of dissolved organic C or KMnO_4 -oxidized OC, was observed to related significantly to microbial respiration rate across sites or soil depths^{11,23}. The amount of labile C inputs to soils may affect organic C decomposition in various ways, e.g., low concentrations labile C input stimulating decomposition while high concentrations C input inhibiting decomposition¹⁷. However, Cheng *et al.*²⁴ found that available C did not limit R_h in the rhizosphere. To clarify the substrate-soil respiration relation, further studies remain needed, especially in natural ecosystems where the input of organic materials (e.g., litter and root exudates) may greatly affect the forms and amounts of substrate availability to respiration.

Traditionally, the first order decay functions that take into account of the temperature and moisture effects are often used in modelling soil respiration^{25,26}. Soil microbial properties including microbial biomass, community composition, and enzyme kinetics are considered important for predicting R_h and SOC storage in recent studies^{25,27,28}, but they are still poorly represented in terrestrial C cycling models²⁹. Comparing with microbial community composition and enzyme kinetics which are complex to assay and hard to parameterize for models, microbial biomass has been firstly targeted in most of microbial-based models²⁹. This is attributable to that, on the one hand, soil microbial biomass *C per se* is an important active SOC pool³⁰ and on the other hand, it is considered as an important agent of SOC sequestration since increasing evidences show that microbial-derived OC contributed greatly to the stable SOC pool³¹. However, Luo *et al.* argued that the first order decay functions should be kept as the backbone of terrestrial C models, since empirical evidences for those complex microbial processes remain rarely observed in natural ecosystems²⁶. Birge *et al.* also suggested to omit microbial biomass from biogeochemical models, based on the results of an incubation experiment³². Whether microbial properties such as microbial biomass dynamics should be incorporated into models remain under debate.

Here, we conducted a field investigation on soil respiration twice per month and other soil physiochemical properties once a month for two years in four subtropical forests of southern China. This region is a significant C sink³³ and therefore potentially important to global C-budget. The studied forests including a pristine broadleaved forest (BF), a secondary mixed coniferous and broadleaved forest (CF), a plantation with coniferous tree species (CP), and a plantation with broadleaved tree species (BP) are representatives of major forest types in the lower subtropical China^{34,35}. This study was conducted with three objectives: the first was to observe seasonal and forest-type R_h variability in the four subtropical forests, the second to explore potential relationships between substrate availability and the R_h variations, and the third to clarify the role of microbial biomass in soil respiration processes. We aimed to provide empirical evidences for whether substrate availability and microbial biomass C should be taken into account in terrestrial C cycling models.

Results

Temporal variations in R_h and environmental conditions. Over the two years, air temperature (T_{air}) recorded in a neighbor weather station exhibited an obvious unimodal seasonal fluctuation in each year, with the average T_{air} being 27.0 °C in the warm-wet season (April to September, termed as warm season hereafter) and 17.3 °C in the cool-dry season (the other months in a year, as cool season hereafter) (Supplementary Fig. S1). Surface soil temperature at 5 cm depth (T_5) observed at our study sites showed a similar temporal pattern and was strongly correlated with T_{air} ($P < 0.001$, Supplementary Figs S1 and S2). In all the forests, T_5 in the cool season was significantly lower than that in the warm season ($P < 0.001$). Although most of the precipitation occurred in the warm season at the four sites (Supplementary Fig. S1), soil moistures at 5 cm depth (M_5) were significantly different between the warm and cool seasons in the BF ($P = 0.045$) and not in the other three forests ($P = 0.101$ for CF, $P = 0.844$ for CP, and $P = 0.159$ for BP; Fig. 1d).

Heterotrophic soil respiration exhibited significant seasonal patterns all the four forests ($P < 0.001$, Fig. 1a and Table 1), which coincided well with T_5 (comparing Fig. 1a with 1b). Consistent with R_h , DOC content showed obvious seasonal patterns over the investigation period ($P < 0.001$, Fig. 1c and Table 1), with higher content in the warm than in the cool season ($P < 0.05$). Other substrate indices including readily-oxidizable organic C (ROC), non-readily oxidizable organic C (NORC), total organic C (TOC), and total nitrogen (TN) changed significantly over time ($P \leq 0.001$, Table 1 and Supplementary Fig. S3), but the magnitude of variations was not as high as that in R_h , T_5 , and DOC (comparing Supplementary Fig. S3 with Fig. 1). In contrast, soil MBC exhibited negligible seasonal fluctuations in the studied forests ($P = 0.204$, Table 1 and Supplementary Fig. S3).

Forest-type variations in R_h and edaphic properties. Average R_h was 1.40, 1.36, 1.08, and 1.23 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for the BF, CF, CP, and BP, respectively (Fig. 2). Respiration rate was significantly lower in the CP than in the BF, CF and BP ($P < 0.05$), but significant difference was not observed in R_h among the latter three ($P > 0.05$, Table 1 and Fig. 2). An exception was in the warm season when significantly higher R_h was observed in the BF than in the BP (Fig. 2). Approximately, annual CO_2 -C released via microbial respiration was 5.2 megagram (Mg) C per hectare per year in these forests (Supplementary Table S2).

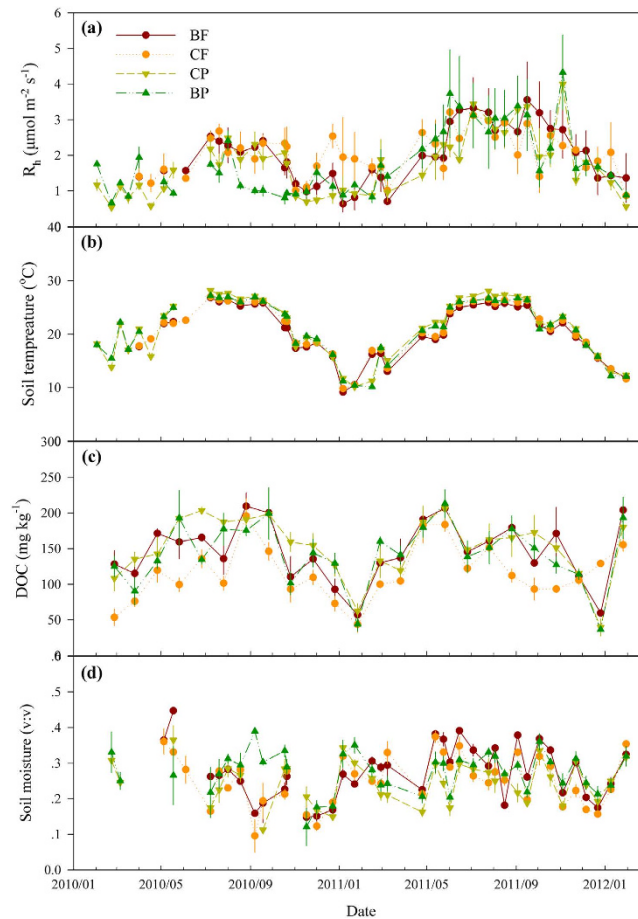


Figure 1. Heterotrophic soil respiration rate (R_h , a), soil temperature (b), dissolved organic carbon (DOC, c), and soil moisture (d) recorded in the four forests over time. Data points are means and error bars represent standard errors ($n = 3$). Measure period ranges from February 2010 through January 2012. The BF is the monsoon evergreen broadleaved forest, CF the mixed coniferous and broadleaved forest, CP the plantation with mixed conifers, and BP the plantation with mixed native broadleaved species. The abbreviations for the four forests (BF, CF, CP, and BP) are the same in the following figures.

Soil temperature was significantly higher in the two plantations (i.e., CP and BP) than in the secondary mixed and primary forests (i.e., CF and BF; $P < 0.001$), whereas moisture was not significantly different among forests ($P = 0.708$, Table 1). Soil substrate content and MBC differed significantly among the forests ($P < 0.05$, Table 1 and Fig. 3). On average, the BF had the highest content of ROC, NROC, TOC, and TN, followed by the BP, CP, and CF orderly ($P < 0.05$, Fig. 3). Soil MBC was also the highest in the BF but lowest in the two plantation forests ($P < 0.05$, Fig. 3). Soil DOC concentration was significantly lower in the CF than in the other three ($P < 0.05$), but did not significantly differ among the BF, CP, and BP ($P > 0.05$, Fig. 3).

Underlying factors relating to the R_h variations. In the four forests studied, soil temperature was the dominant influential factor controlling the seasonal R_h variations, of which 45–85% was explained by T_5 changes with exponential functions ($P < 0.001$, Fig. 4). Soil moisture did not show a significant relationship with R_h in any of the forests within our investigation period ($P > 0.05$). Besides soil temperature, DOC content was also significantly related to the seasonal R_h variations in these forests ($P < 0.05$) except for the BP ($P = 0.425$, Fig. 4), but such significant relationships did not maintain ($P > 0.05$) after removing the temperature effect on R_h firstly employing statistical techniques (i.e., partial mantel test and partial correlation analysis). No significant correlations was detected between R_h and the other substrate indices in the cool and warm seasons, or the whole period ($P > 0.05$, Supplementary Fig. S4). Neither did microbial biomass C show a significant correlation with the seasonal R_h variations in any of the studied forests ($P > 0.05$, Supplementary Fig. S4).

Across the forests, no significant correlations were observed between R_h and substrate content or C/N ratio, either in the cool or warm season ($P > 0.05$, Supplementary Fig. S5). Microbial biomass C was significantly related to R_h in the warm season ($P = 0.043$, Fig. 5). At presence, specific respiration rates and microbial respiration quotient were calculated to indicate decomposability of OC and microbial metabolic activity^{23,36,37}. Results showed that decomposability of DOC was significantly related to R_h across the forests in the warm season ($P = 0.003$), and marginally significant in the cool season ($P = 0.063$, Fig. 5). However, no significant relationships were detected

		Forest	Time	Forest & Time
R_h	<i>F</i>	10.26	21.46	1.53
	<i>P</i>	0.004	<0.001	0.162
T_5	<i>F</i>	79.36	9870.7	92.3
	<i>P</i>	<0.001	<0.001	<0.001
M_5	<i>F</i>	0.48	56.93	4.81
	<i>P</i>	0.708	<0.001	<0.001
MBC	<i>F</i>	66.64	1.6	2.42
	<i>P</i>	<0.001	0.204	0.028
DOC	<i>F</i>	8.26	24.59	2.01
	<i>P</i>	0.008	<0.001	0.043
ROC	<i>F</i>	36.98	5.07	1.59
	<i>P</i>	<0.001	0.001	0.12
TOC	<i>F</i>	50.4	8.41	2.18
	<i>P</i>	<0.001	<0.001	0.020
TN	<i>F</i>	93.71	10.42	1.83
	<i>P</i>	<0.001	<0.001	0.064

Table 1. Results of repeated measures ANOVA on heterotrophic soil respiration (R_h) and the according soil properties across the forests over time. Numbers represent statistical *F* and *P* values, with bold indicating significant differences at $P < 0.05$. In the table, T_5 and M_5 are soil temperature and moisture at 5 cm depth, MBC microbial biomass carbon (C), DOC dissolved organic C, ROC readily-oxidizable organic C, TOC total organic C, and TN total nitrogen content.

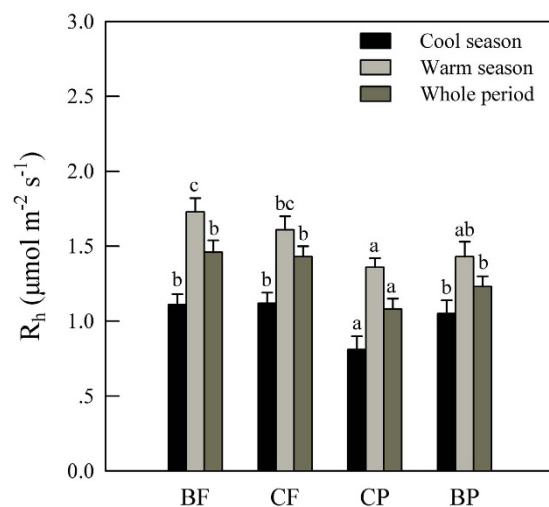


Figure 2. Average heterotrophic soil respiration rate (R_h) at seasonal and measurement-period scales in the four forests. Vertical columns are means and error bars represent standard errors. Different letters above bars indicate significant differences at $P < 0.05$ among forests on the same time scale. The warm season ranges from April to September, while the other months in a calendar year compose the cool season.

between R_h and decomposability of ROC and TOC ($P > 0.05$). Microbial respiration quotient did not show significant correlation with R_h in either of the seasons ($P > 0.05$).

Discussion

In these subtropical forests, CO_2 originated from microbial decomposition on average accounted for 60% of the total soil respiration, which was approximately $8.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (Wei *et al.*, unpublished data). The annual R_h and its percentage to R_s observed in the present study are in the range reported by previous studies^{5,38} but a bit higher than the corresponding averages of global subtropical ecosystems ($4.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ and 53%, respectively)⁵. However, subtropics constitute of humid and semiarid/arid ecosystems, with the former predominated by evergreen broadleaved forests while the latter by savannas or deserts³⁹. Therein, soil respiration in humid broadleaved forests is significantly higher than that in arid ecosystems such as savanna⁴⁰ and the relatively higher R_h in this study may be attributable to sufficient supply of water and heat in these forests³⁴, which is beneficial for microbial activities and SOM decomposition. Moreover, different vegetation productivity in these subtropical ecosystems^{39,40},

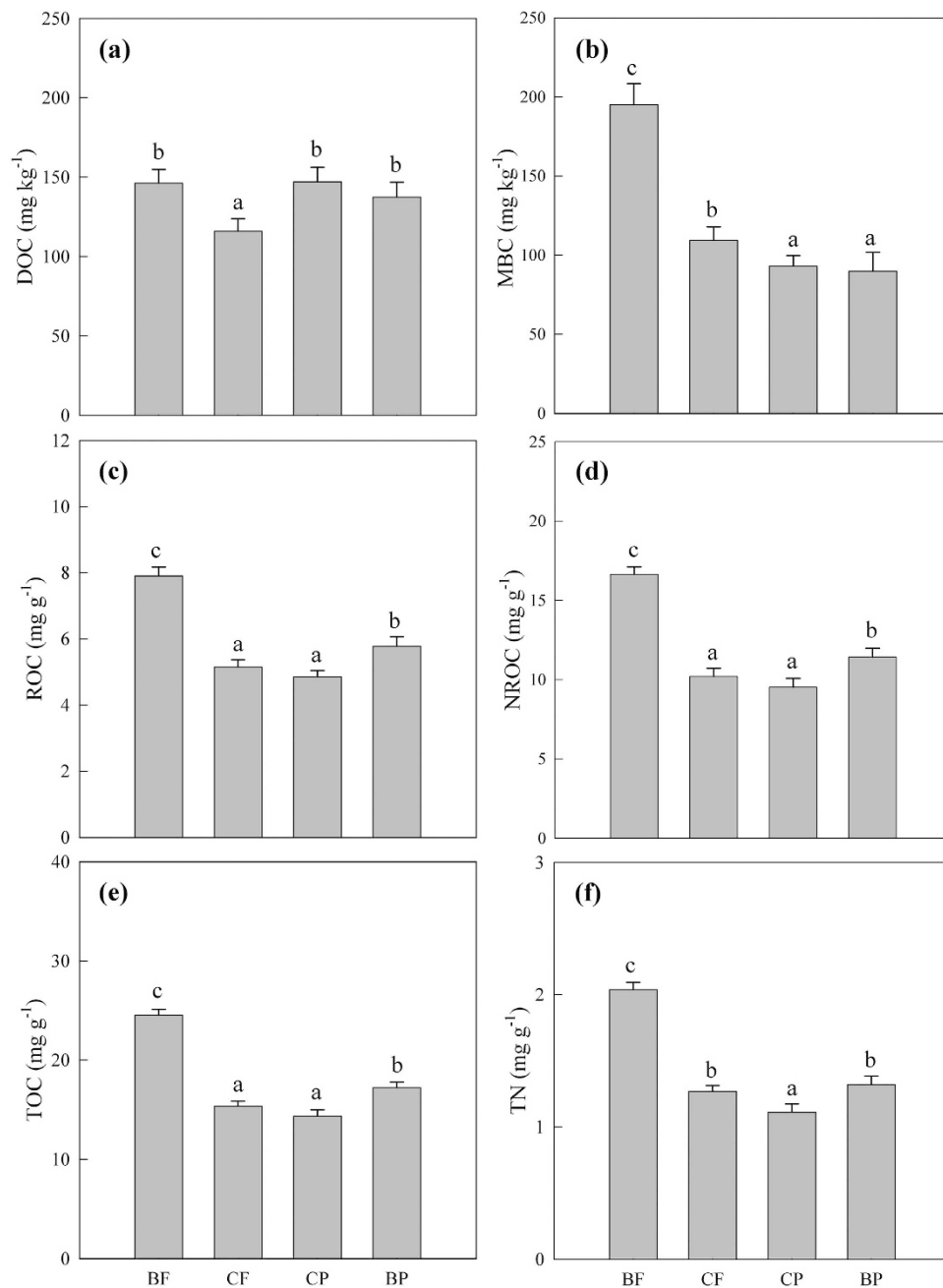


Figure 3. Average soil carbon (C) and nitrogen (N) content and microbial biomass C (MBC) in the four forests. Vertical bars are means within the 2-year measurement period and error bars represent standard errors ($n = 24$). Different lowercase letters above bars indicate significant differences at $P < 0.05$ in each panel. DOC is dissolved organic C, ROC readily-oxidizable organic C, NROC non-readily oxidizable organic C, TOC total organic C, and TN total nitrogen.

consequently different qualities and quantities of organic C substrates input into soil, could also contribute to the discrepancy between this study and the global average R_h .

One aim of this study was to detect R_h variability on the temporal and spatial scales in the four subtropical forests. As shown, heterotrophic soil respiration exhibited obvious seasonal rhythms in all of the forests studied (Fig. 1a). Our results indicated that soil temperature was the predominant influential factor driving the seasonal R_h variations. This exponential relationship between both is well consistent with previous soil respiration studies^{10,41,42}. Theoretically, temperature rises within a certain range can stimulate metabolism activities and maintenance respiration of soil microorganisms⁴³; both processes would result in elevated R_h .

Soil water supply can influence soil respiration in many ecosystems^{8,9,44}, but relationships between the two are diverse^{9,44,45}. For example, linear, exponential, and quadratic functions have been used to fit the relationships between soil respiration and moisture previously^{9,45}. However, we did not observe an obvious moisture effect on

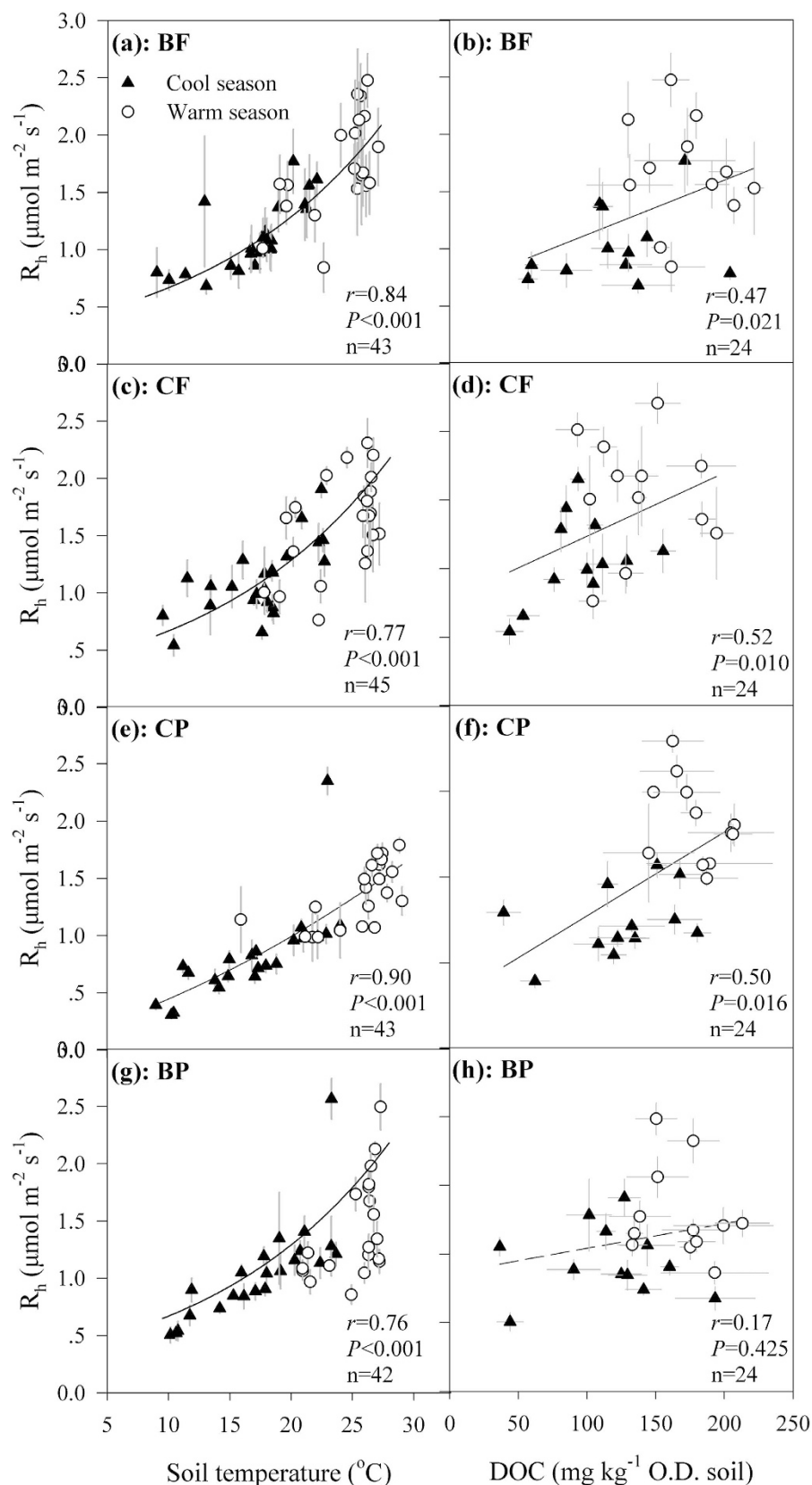


Figure 4. Relationships between soil temperature or dissolved organic carbon (DOC) and heterotrophic soil respiration (R_h) in the four forests. Plots are means and error bars represent standard errors ($n=3$). Solid lines indicate significant relationships between the two variables. Statistical Pearson coefficients r , P value and number of samples are shown in each panel. In prior to correlation between temperature and R_h , R_h was ln-transformed due to the obvious exponential relationship between both. O.D. soil in the unit of DOC is the abbreviation of oven-dried soil.

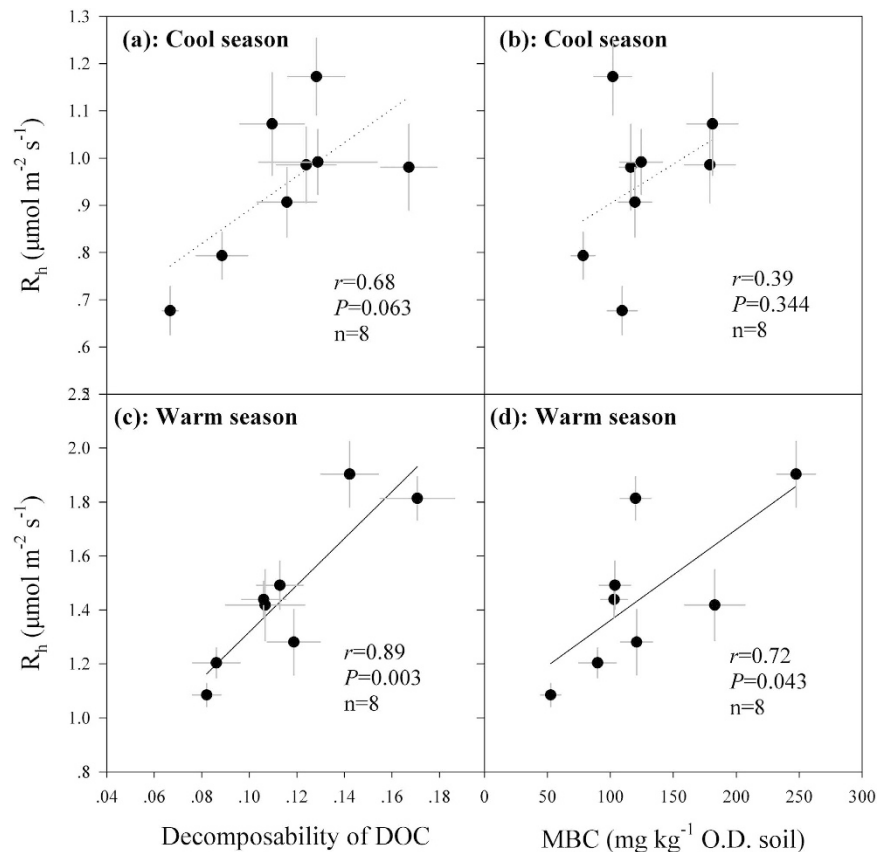


Figure 5. Correlations between heterotrophic soil respiration (R_h) and decomposability of dissolved organic carbon (DOC) or microbial biomass carbon (MBC) across the four forests in the cool or warm season, respectively. Plots represent means in the cool or warm season in each year and error bars represent standard errors ($n = 6$). Solid lines indicate significant relationships at $P < 0.05$ while dashed lines indicate insignificant relationships. Statistical Pearson coefficients r , P value and number of samples are shown in each panel.

R_h . That may be attributed to the relatively high soil moisture recorded within our investigation period (averagely 27%, 29%, 29%, and 28% in the BF, CF, CP, and BP, respectively). Even in the cool season with less precipitation, average M_5 was 26%, 29%, 27%, and 27% for the four forests, respectively. Soil respiration variations may be more determined by soil moisture as far as it exceeds a specific lower (e.g., 15%)⁴⁶ or upper threshold⁸, which depends greatly on soil properties⁴⁴. Soil moisture at our sampling points may have rarely reached the threshold to limit the activity of soil microorganisms, just as in some previous studies^{8,47,48}. Therefore, the relatively high M_5 may explain the absence of moisture effect on soil respiration observed in this study.

Another aim of our study was to verify the relationship between substrate availability to the R_h variability under field conditions. To date few studies have related periodically-measured R_h to the corresponding soil substrate (but see Iqbal *et al.*²¹), despite that substrate supply has been considered a marked influential factor on soil respiration^{12,19,49}. Therefore, we assayed different forms of SOC together with R_h in these subtropical forests to reveal direct linkages between the two. In this study, DOC was chosen as an index of soil labile C supply^{23,50,51}, since it could support a great proportion of microbial activity in soils^{52,53}, especially in the initial stage after it enters the soil⁵⁰, and respiration $\text{CO}_2\text{-C}$ was observed to originate from DOC⁵⁴. We recognized that part of DOC in mineral soils could originate from decomposition of litter and SOM⁵³, implying that DOC, at least in part, was likely products of SOM decomposition, but other processes such as leaching of soluble organic materials from litter, root exudations, and microbial cell lysates could also contribute to DOC pool in soils^{52,53}. As results showed, the positive correlation between DOC content and R_h indicates that the amount of soil substrate supply may positively affect microbial respiration, with higher DOC content stimulating microbial respiration. Notably, however, this significant relationship between R_h and DOC by simple correlation analysis did not maintain after removing the compound effect of temperature on R_h employing statistically partial mantel test or partial correlation analysis, taking into account that soil temperature also fluctuated consistently with DOC content within the period. This would not completely deny the underlying effect of DOC content on R_h but highlights the confounding effects of multi-variables on soil respiration in field, and therefore the pattern needs to be interpreted with care. How to efficiently differentiate the compound effects of targeted and synergetic variables has been a challenge in field studies.

Dissolved OC quality, indicated by decomposability of DOC^{23,36,37}, was found to affect R_h significantly across forests. Soil microorganisms may incorporate high-quality DOC efficiently into their biomass; this means that with the equal amount of DOC supply, less C would be emitted as CO_2 in high vs. low quality DOC. However, the

significant correlation between them was observed only in the warm but not the cool season, possibly due to some other variables interactively affecting R_h with the quality of DOC in the cool season and therefore shadowing its role then. Soil ROC was another index employed to indicate substrate availability, as it is highly labile for decomposition and sensitive to reveal changes in pool size⁵⁵. Nevertheless, we did not observe a significant correlation between ROC and R_h in any forest. Soil DOC is a preferable predicting variable for microbial respiration over ROC, NROC, and TOC, possibly due to it being highly movable and thus easily-available to soil microorganisms⁵⁴. These observations prove that soil substrate availability contributes to the R_h variations to a certain extent in forests. However, we cannot rule out the possibility that the good correlation between DOC content and R_h is attributable to that both of DOC and CO_2 are products of SOM decomposition in this study. Further studies using isotope tracing technique to clarify the relationship between DOC and respired CO_2 -C could improve our understanding on this topic.

Although both soil temperature and DOC content showed positive correlations with R_h in these forests, neither of them could explain the R_h variations across the four forests. Instead, soil TOC and its readily-oxidizable fraction, as well as TN and microbial properties, may be associated with the R_h differences among the four forests. For example, the highest R_h in the BF corresponded with the highest substrate supply, since the concentrations of soil TOC, ROC, and TN were significantly higher in the BF than in the other forests. Higher R_h in the BF may also be ascribed to its higher MBC compared with the other forests, because MBC was significantly related to R_h (Fig. 5d; see also Wang *et al.*¹¹). Similarly, the R_h differences between CP and CF or BP are likely attributed to the lower MBC or substrate supply in the CP. Moreover, we consider that OC decomposability may also contribute to the observed R_h variations among forests. Soil microbes with low C use efficiency (CUE) may exhibit higher R_h even when less substrate is supplied^{56,57}, because they incorporate SOC into their biomass with low-efficiency. We did not measure CUE directly but the decomposability of OC may indicate microbial CUE indirectly, with higher R_h /OC implying lower CUE. As expected, the CF had the highest decomposability of OC, implying that soil microbes in CF had the minimum efficiency in incorporating OC into their biomass. In other words, they contain higher efficiency in converting OC into CO_2 , which may explain why the CF with lower substrate supply had higher R_h than that in BP. Assays in microbial community composition with C use efficiency/preference would provide stronger evidences for this speculation but unfortunately, they were not covered in the present study.

Moreover, our results suggest that incorporating MBC into terrestrial C cycling models may improve the prediction accuracy for R_h , but this would not be always the case since we observed a significant correlation between MBC and R_h only in the warm season. This partially supports to take MBC into account when modeling soil respiration^{29,30}. However, in specific ecosystems or under specific environmental conditions, MBC could only be a minor factor controlling R_h when some other variables influence R_h greater over MBC³². Empirical evidences remain insufficient to verify underlying importance of microbial properties on soil respiration in natural ecosystems²⁶, although the results of this study increase the profile for supporting to incorporate MBC in terrestrial C cycling models. Additionally, the observations in the present study that significant correlations between R_h and MBC or the decomposability of DOC occurred in the warm season but not in the cool season highlight the complexity to explore influential factors controlling soil respiration in field, as differed variables may play roles on affecting R_h within different periods even in one ecosystem⁴⁵, and this is true in different ecosystems^{17,18,24}. There remains a challenge to establish a versatile model for predicting soil respiration accurately under different conditions in various ecosystems, because it is always hard for the selection of optimized parameters to balance the accuracy and utility of models³⁰.

In summary, heterotrophic soil respiration showed obvious temporal and forest-type variations in these subtropical forests within our investigation period. Temperature was the dominant factor controlling R_h variations in these forests. Soil moisture did not affect R_h within our investigation period since the water supply rarely went beyond or below the thresholds to limit microbial activities. In spite of the confounding effects with temperature, soil substrate availability may be also an important influential factor controlling soil respiration, as indicated by the synchronical seasonal changes in DOC content and R_h and the preferable correlation between R_h and DOC over ROC, NROC, or TOC. Moreover, incorporating MBC into C cycling models could improve the prediction of R_h variations but it depends case by case. Further empirical studies combining incubation experiments and field observations remain needed to explore how substrate availability and microbial properties affect R_h .

Methods

Site description. Field investigations were conducted in four subtropical forests in Guangdong province, southern China. The BF and CF forests are situated in the Dinghushan Biosphere Reserve (DBR; 112°30' ~ 112°33'E, 23°09' ~ 23°11'N), and the CP and BP plantations are located at the Heshan National Field Research Station of Forest Ecosystems (HSF; 112°54'E, 22°41'N), which is about 70 km away from the DBR. Both sites experience subtropical monsoon climate, with average air temperatures of 22.3 °C in the DBR and 21.7 °C in the HSF^{58,59}. Average annual precipitation amount is 1678 mm in the DBR and around 1700 mm in the HSF, of which about 80% falls in the warm season ranging from April to September^{58,59}. The remaining 20% precipitates in the other months in a calendar year which compose the cool season. Soil in both sites is acidic and classified as oxisols in the USDA soil taxonomy^{34,35}.

The BF is the regional climax vegetation in lower subtropical China. Due to the protection by Buddhist monks in a nearby temple, the BF under study has developed naturally for about 400 years³⁴. The CF has developed gradually from a planted coniferous forest with the invasions of pioneer broadleaved species since it was free from human disturbances 70 years ago³⁴. The stand age of CF is around 100 years old. The dominant tree species are *Castanopsis chinensis*, *Schima superba*, *Cryptocarya chinensis*, *Machilus chinensis*, and *Syzygium rehderianum* in the BF and *Pinus massoniana* and *S. superba* in the CF^{10,19,34}.

Before plantation, the HSF site was a homogenous degraded hilly land with similar soil property and species composition. The BP (2.68 ha) and CP (3.17 ha) were established in 1984 to experimentally demonstrate forest

restoration in such degraded hilly land in southern China. In each of the plantations, trees were planted at a spacing of 3×2.5 m, with the dominant species being *P. massoniana* and *Cunninghamia lanceolata* in the CP, and *S. superba* and *Cinnamomum burmanii* in the BP^{59,60}. The species have been typically used for forest restoration in the hilly area of southern China and accounted for considerable proportions of plantation forests in this region³⁵.

Supplementary Table S1 lists major vegetation and soil properties of the four forests under study. In comparisons with the two plantations, the BF and CF had higher stem density, diameter at breast height (DBH), litterfall, and root biomass (Supplementary Table S1). In terms of coverage, tree height and aboveground net primary production (ANPP), the 25-year-old broadleaved species mixed plantation (BP) was close to the older primary and secondary forests (i.e., the BF and CF). Soils at the DBR sites had higher clay content, dissolved inorganic nitrogen (DIN) but lower available phosphorous (P) content (Supplementary Table S1).

Field measurements. Three 10×10 m² quadrats were established in each of the four forests. Each quadrat contained three 1×1 m² plots, which were trenched for measuring R_h . Trenching was conducted as follows. Briefly, four sides of each trench plot were dug and double-layer nylon net (100 meshes) used to cover the outside edges of trench plots. Then soil was refilled to the trenches accordingly. The depth of trenching was 50 cm in the BF and CF unless base rock was reached, and 50–70 cm in the CP and BP. A previous study observed that the most roots (<5 mm) distributed in the soils of 0–40 cm depth in forests in the study site, and therefore this depth was considered as main lateral root zone in these forests⁶¹. Moreover, some of the trenches were down to base rock when established, especially in the CF. We therefore considered that in the present study, trenches were deep enough to exclude the most of lateral root respiration which accounted for the largest proportion of total root respiration⁶². In spite of lateral diffusion of root respired CO₂ into trenches likely resulting in overestimation on R_h ⁶³, nylon net was used to prevent roots from growing into those trenched plots while minimizing interruption on laterally water and nutrient exchanges; soil conditions in such trenches were closer to nature than that in trenches isolated by PVC panels since the latter was more likely to change soil conditions, e.g., water content in trenched plots and nutrient exchanges between trenched and their neighboring areas. In each plot, one 20×5 cm PVC collar (diameter \times height) was inserted into soil, with the upper 2 cm sticking out above soil surface, and left *in situ* throughout the whole measurement period. Trenching and collar installations were conducted in November 2009. Small plants in these trenched plots were removed frequently in order to exclude R_a .

Soil respiration rate was measured in each plot using a portable CO₂ analyzer (Li-8100 Auto Soil CO₂ Flux System, Li-Cor Biosciences, NE, US) for two years from February 2010 to January 2012, with a frequency of twice per month (normally on rainless days at the start and in the middle of a month). With auxiliary temperature and moisture sensors, soil temperature and moisture at 5 cm depth were recorded at the same time. At each sampling time, soil respiration rate was measured between 9:00 and 12:00 a.m. local time, during which the measured respiration rate was approximate to the daily averages in the study site^{19,34}.

Soil collections and analyses of soil properties. A circular soil auger (4×20 cm²; inner diameter \times length) was used to collect soil samples in the trenched plots monthly at the second measuring time for R_h each month. For each sampling occasion, samples from the same quadrat were mixed homogeneously to form a composite sample for lab analyses. Thus, we finally had three soil samples per stand each time.

Prior to soil assays, visible stones and roots were picked out and samples were sieved through a 2-mm mesh. Each sample was then separated into two parts, in which the first was used to determine DOC and MBC and the second air-dried and further ground to test ROC, TOC, and TN. In brief, MBC was assayed by fumigation-extraction-back titration method and calculated with an extraction coefficient of 0.38, following Vance *et al.*⁶⁴. The K₂SO₄-extracted OC concentration in non-fumigated soils indicated DOC, which was a proxy of soil substrate availability⁵¹. ROC was determined using a wet oxidizing method with 0.333 M KMnO₄, as described in Blair *et al.*⁵⁵. TOC was analyzed with the Walkley-Black method and TN with the micro-Kjeldahl method⁶⁵. Difference between TOC and ROC in each sample was content of NROC.

Statistical analyses. Heterotrophic soil respiration rate in the same quadrat was averaged at each sampling occasion ($n = 3$) in prior to further analyses such as correlations and analysis of variance (ANOVA). To explore underlying influences of substrate quality on the R_h variations across forests, specific respiration rate was calculated via dividing respiration rate by content of organic carbon (OC)²³, i.e., $\mu\text{mol CO}_2\text{-C}$ release per unit of OC, which reflected decomposability or quality of OC^{36,37}, as well as microbial decomposition efficiency in soils²³. The ratio of R_h over the corresponding DOC, ROC or TOC content was calculated in this study to indicate decomposability of OC^{23,36,37,66}. This normalization process could cancel substrate quantity-induced differences in R_h and shed lights on effects of substrate quality on R_h ^{23,36,37}. Microbial respiration quotient, i.e., the R_h per unit of MBC, was calculated to indicate metabolic status of soil microbes^{66,67}. Repeated measures ANOVA were used to detect differences in respiration rate and soil physiochemical properties among forests over time. One-way ANOVA was also performed to explore significant difference of average R_h and edaphic properties across forests. Tukey HSD multiple comparisons were employed when difference was significant. Bivariate correlation was used to test potential relationships between R_h and soil properties. Taking into account of predominant effect of temperature on R_h over other environmental and soil physiochemical and microbial properties, partial correlation and partial mantel analyses were also employed to statistically check the relationships between R_h and soil properties when excluding their confounding effects with temperature. Data were tested for normality and heterogeneity of variance in prior to ANOVAs and correlations. Logarithm- or rank-transformation was performed once H_0 assumption was rejected. For all the statistics, significance level was set at $P < 0.05$. All the statistical analyses, except for partial mantel tests conducted in R software (version 3.1.2), were finished in SPSS 16.0 for windows (SPSS Inc., Chicago, US) and graphs made in SigmaPlot 10.0 (Systat Software Inc., California, US).

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Author Contributions

H.W. and X.C. contributed equally to this work. W.S. conceived the study. H.W., X.C. and G.X. carried out the field measurements and soil assays. H.W., X.C., B.G., S.V. and W.S. contributed to data analyses, result explanations, and manuscript writing and revision.

Additional Information

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