RESEARCH ARTICLE

Soil respiration in a subtropical forest of southwestern China: Components, patterns and controls

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Abstract

Partitioning the components of soil respiration is crucial to understand and model carbon cycling in forest ecosystems. In this study, total soil respiration (R_s), autotrophic respiration (R_A), heterotrophic respiration (R_H), litter respiration (R_L), litterfall input and environmental factors were synchronously monitored for 2 years in a subtropical Michelia wilsonii forest of southwestern China. R_H rates were often higher than R_A rates during the two years except for the middle growing season (from July to September). The mean rate of R_S, R_A, R_H and R_L was 1.94 μmol m⁻¹ s⁻¹, 0.85 μmol m⁻¹ s⁻¹, 1.09 μmol m⁻¹ s⁻¹ and 0.65 μmol m⁻¹ s⁻¹, respectively, during the 2-year experiment. Annual CO2 emission derived from R_A, R_H and R_L was 3.26 Mg C ha⁻¹ a⁻¹, 4.67 Mg C ha⁻¹ a⁻¹ and 2.61 Mg C ha⁻¹ a⁻¹, respectively, which accounted for 41.4%, 58.6% and 32.9% of R_S. Over the experimental period, the ratio of R_H/R_S increased with soil temperature but the opposite was true for R_L/R_S. The Q10 value was 2.01, 4.01, 1.34 and 1.30, respectively, for R_S, R_A, R_H and R_L. Path analysis indicated that environmental variables and litterfall production together explained 82.0%, 86.8%, 42.9% and 34.7% variations of monthly fluxes of R_S, R_A, R_H and R_L, respectively. Taken together, our results highlight the differential responses of the components of R_S to environmental variables.

Introduction

Soil respiration (R_S) is the second largest flux of carbon dioxide (CO2) between terrestrial ecosystems and the atmosphere [1, 2]. R_S accounts for roughly 80% of ecosystem respiration across global forests [3]. In general, R_S is largely controlled by environmental factors, including temperature and moisture [4]. Moreover, R_S is complicated by tree growth and the subsequent input of plant litter to soil [5, 6].

R_S is overwhelmingly the product of respiration by plant roots (autotrophic respiration, R_A) and soil organisms (heterotrophic respiration, R_H) [7, 8]. In addition, CO2 flux derived from decaying litter accounts for a considerable part of R_S, which is strongly controlled by the quantity and quality of litter and climate variables [5, 8, 9]. A recent meta-analysis indicated that
aboveground litter removal and root removal declined $R_s$ by 22.8% and 34.1%, respectively [6]. Soil temperature is one of the most important factors that control the variations of $R_s$ in terrestrial ecosystems but the size of this effect is dependent on system types and climate zones [10, 11]. Soil moisture also mediates the temporal and spatial pattern of $R_s$ [4, 12]. Both $R_A$ and $R_H$ generally increased with temperature and precipitation across global forest ecosystems [4]. However, moisture effect may be complicated by the effects of soil temperature and other factors [13, 14]. Different components of $R_s$ could be dominantly mediated by different mechanisms, such as substrate quality, plant traits and environmental factors. Obviously, partitioning the components of $R_s$ and exploring the relative importance of biotic and abiotic factors on each component is very helpful for understanding the mechanistic of soil carbon cycling.

Chinese subtropical forests have high biomass and productivity, which play an important role in the carbon storage of global terrestrial ecosystem [15]. Over last decades, almost all natural forests in subtropical China have been deforested due to demand for timber, and subsequently often reforested with fast-growing tree species. So far, previous studies focused mainly on the plantations dominated by non-native fast-growing tree species, such as Pinus massoniana and Cunninghamia lanceolata [16, 17]. However, the components of $R_s$ and its controls have been scarcely investigated in the restored forests dominated by native tree species in this region. In this study, we investigate the components of $R_s$ for two years using root trenching and litter exclusion techniques in a subtropical Michelia wilsonii (a special native tree species) forest of southwestern China. The specific objectives of this study were (1) to explore the seasonal dynamics of each respiration component; (2) to assess the relative importance of biotic and abiotic factors for temporal patterns of each component.

Materials and methods

Ethics statement

We received a permission from the Dujiangyan Bureau of Forestry to conduct this experiment in the studied forest in 2015. In this study, only limited soil samples were collected to measure physical and chemical properties and PVC chambers were set up to monitor soil respiration. Our work had negligible effects on the function of the broader ecosystem. Additionally, this study was carried out in compliance with the laws of the People’s Republic of China. This study did not involve measurements of humans or animals, and no endangered or protected plant species were involved.

Site description

The site is conducted in the Dujiangyan Experimental Forest of Sichuan Agricultural University, southwestern China (103° 37’ E, 30° 59’ N, 911 m asl). This area is characterized by a mid-subtropical, humid, mountainous climate that produces the wet season from May through October and the dry season from November through April. The mean annual temperature and precipitation is 15.2˚C and 1 243 mm, respectively. The dominant tree species is Michelia wilsonii and the understory are Lespedeza bicolor, Pittosporum glabratum, Dranceopteis dichotome and Cyperus rotundus, respectively. The soil is classified as ferralsol with old alluvial yellow loam according to the Chinese Soil Taxonomy (RGCST 2001). The basic topsoil properties (0–20 cm) as determined in August 2016 are as follows: organic C 15.76 g kg$^{-1}$, total N 1.92 g kg$^{-1}$, total P 0.32 g kg$^{-1}$, and pH 5.73. Neither fertilization nor drainage had been carried out since tree establishment in the stand. Moreover, the topography is relative flat (less than slope 10˚) and tree canopy coverage is about 0.9.
Experimental design

In August 2015, five 10 m × 10 m replicate plots were established in the experimental site. There were three treatments: control [C] (undisturbed), No-Roots [NR] (root growth excluded) and No-Litter [NL] (aboveground litter excluded). In each plot, a trench subplot was set up with a dimension of 1 m × 1 m. For the trenched subplots, we dug a trench of 0.2 m width and 0.6 in depth. The polyethylene films (37 μm mesh size) were placed along the bottom and sides of the trenches to prevent roots from entering the trench. The excavated soil was gently backfilled into the trench according to its initial profiles to minimize disturbance. Existing litters in the NL plots (1 m × 1 m) were removed and litterfall was excluded by pyramid-shaped screens (1-mm mesh) placed approximately 1 m aboveground. All litters fell around the NL plots were monthly removed before the measurements of soil respiration.

The trenching method was applied to divide \( R_S \) into \( R_{H} \) and \( R_{A} \), the litter removal was used to calculate the respiration derived from aboveground litter decomposition. We calculate the soil respiration fractions from each source as follows:

\[
\text{Heterotrophic respiration (} R_H \text{)} = \frac{\text{Control plots}}{\text{NR plots}}
\]

\[
\text{Autotrophic respiration (} R_A \text{)} = \frac{\text{Control plots}}{\text{NR plots}}
\]

\[
\text{Litter respiration (} R_L \text{)} = \frac{\text{Control plots}}{\text{NL plots}}
\]

Soil respiration measurements

In each treatment plot, one polyvinyl chloride collar (PVC) (diameter of 20 cm and height of 8 cm) was permanently installed 2–3 cm deep into soils to measure soil respiration. All vegetation inside the collar had removed artificially before monitored soil respiration. To minimize the response caused by transient decomposition of dead roots, the initial measurements of soil respiration was carried out 3 months after trenching treatment was conducted. From November 2015 to October 2017, soil respiration was measured every month using an automated soil respiration system (Li-8100, Li-Cor Inc., Lincoln, NE, USA). Soil respiration was measured between 9.00 a.m to 12:00 a.m (Beijing time). At the same time, soil temperature (°C) and moisture (v/v) at the depth of 5 cm was synchronously measured by the probes connected to Li-8100 system.

Microclimate and litterfall measurements

Rainfall, air temperature (\( T_{\text{air}} \)) and soil temperature (\( T_{\text{soil}} \)) were constantly measured using HOBO Micro Station Data Loggers (Onset Computer Corporation, Bourne, Massachusetts, USA) located adjacent to the experimental area. Forest aboveground litter was collected using six circular litter traps in each plot. The litter traps were funnel shaped with the diameter was 1 m and the collection area was 0.785 m². During the monitoring period, each trap was collected monthly, then collected litter was oven-dried at 65°C to a constant mass for 48 h, and weighed.

Statistical analyses

Based on the measured data, an exponential model was performed to describe the relationship between soil respiration fractions and soil temperature [18]:

\[
R_S \text{ or } R_A, R_H, R_L = a \times e^{\beta \times T}
\]

Where \( R \) was soil respiration rate (\( \mu \text{mol m}^{-2} \text{s}^{-1} \)), \( T \) was soil temperature (°C), coefficient \( \alpha \) is the intercept of soil respiration when temperature is zero, and coefficient \( \beta \) represents the temperature sensitivity of soil respiration. Based on the continuous soil temperature at the 5
cm depth, monthly and annual soil CO₂ fluxes of each fraction was estimated by integrating CO₂ fluxes for the period from November 2015 to October 2017 using the observed specific response equation between soil respiration fraction and soil temperature. Monthly and annual soil CO₂ fluxes of each fraction was estimated by interpolating measured soil respiration between sampling dates for every day of the year and then computing the sum to obtain the annual or winter values [19].

Structural equation models (SEM) were used to assess the holistic effect of measured variables on monthly fluxes of each respiration component. In the model, monthly soil respiration emission of each component was the response variable. Monthly mean air and soil temperature, monthly precipitation (MP), litterfall production, soil moisture were variables. The normality of data distribution was examined for heteroscedasticity, and all bivariate relationships were checked for signs of nonlinearities before the SEM analysis. These analyses were performed by using the maximum-likelihood estimation. Model fit was considered good when the χ² test was low (< 2) and its associated p-value was high (> 0.05). The Bentler’s comparative fit index (CFI) and Bentler-Bonett normed fit index (NFI) were used to evaluate the adequacy of fit. For each set of analysis, R² values were obtained for each dependent matrix, representing the proportion of total variance explained by the model. All statistical analyses were carried out in SPSS version 20.0 for Window (SPSS Inc, Chicago, Illinois, USA). Graphs were generated using SigmaPlot 12.5 software (Systat Software, Inc., San Jose, CA, USA). Significance was determined at α = 0.05.

Results

Microclimate and litterfall

Both air and soil temperature showed a clear seasonal dynamic (Fig 1A). Average air temperatures was 14.6˚C and 14.9˚C, respectively, in 2016 and in 2017; likewise, mean soil temperatures was 15.1˚C in 2016 and 17.9˚C in 2017. Rainfall was 872.8 mm and 944.8 mm, respectively, in 2016 and 2017. Similar to air temperature, it was higher in summers but lower in winters (Fig 1B). However, there was no obvious seasonal variation in soil moisture and a minimum was observed in June of both years (Fig 1B). Annual aboveground litterfall was 312.0 g m⁻² a⁻¹ in 2016 and 352.2 g m⁻² a⁻¹ in 2017 (Fig 1C). In general, the amount of litterfall was significantly greater in the winter (November and December) as compared to other seasons (Fig 1C).

Soil respiration components

The rates of all soil respiration components had obvious seasonality, with the maximum in summer and the minimum in winter (Fig 2A). The mean annual rates of Rs, Ra and Rh was 1.94 μmol·m⁻²·s⁻¹, 0.85 μmol·m⁻²·s⁻¹ and 1.09 μmol·m⁻²·s⁻¹, respectively, throughout the experimental period (Table 1). In general, Rh was higher than Ra over the year. However, the opposite tendency was observed from June to August.

During the two years, the proportion of Ra to Rs (Rs/Ra) ranged from the maximum 70.6% in summer to the minimum 16.6% in winter, whereas the proportion of Rh to Rs (Rh/RS) showed the opposite pattern (Fig 2B). The proportion of RL to Rs (RL/RS) varied from 14.1% to 67.5%. Annual CO₂ emission derived from Rs, Ra, Rh and RL was 7.93 Mg C ha⁻¹ a⁻¹, 3.26 Mg C ha⁻¹ a⁻¹, 4.67 Mg C ha⁻¹ a⁻¹ and 2.61 Mg C ha⁻¹ a⁻¹, respectively (Table 1). There was a positive logarithmic relationship between Ra/RS and soil temperature (Fig 3A, P < 0.001). Conversely, both Rh/RS and RL/RS decreased with increasing soil temperature (Fig 3B and 3C, P < 0.01).
Correlations between environmental variables and soil respiration components

$R_L$, $R_S$, $R_A$ and $R_H$ rates all exhibited an exponential correlation with soil temperature (Fig 4). Correspondingly, the $Q_{10}$ values of $R_S$, $R_A$ and $R_H$ were 2.01, 4.01 and 1.34, respectively (Fig 4A–4C). Moreover, the $Q_{10}$ value of $R_A$ was higher than those of $R_H$ and $R_L$.

Fig 1. Seasonal variations of air and soil temperatures (a), precipitation and soil moisture (b), and litterfall (c) in the Michelia wilsonii plantation of southwestern China.

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Fig 2. Seasonal variations of components of soil respiration rates (a) and its percentage (b) in the Michelia wilsonii plantation of southwestern China.

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Path analysis showed that measured variables together explained the variation of 82.0%, 86.8%, 43.0% and 34.6%, respectively, in monthly flux of $R_S$, $R_A$, $R_H$ and $R_L$ (Fig 5). Total, direct and indirect effects of the environmental variations were summarized in Fig 5. $T_{air}$ and rainfall were strongly associated with monthly flux of $R_S$ and $R_L$ (Fig 5A and 5D). Moreover, $T_{air}$ had an indirect effect on monthly flux of $R_S$ (0.26), $R_A$ (0.77) and $R_H$ (0.41) via $T_{soil}$, litter-fall and moisture (Fig 5A–5C). Soil moisture had a significant negative effect on $R_S$ (-0.31), $R_H$ (-0.54) and $R_L$ (-0.22) (Fig 5A, 5C and 5D).

**Discussion**

**Annual C release and variations through soil respiration components**

Previous synthesis showed that annual mean total CO$_2$ efflux was 3.22 Mg C ha$^{-1}$ a$^{-1}$, 6.62 Mg C ha$^{-1}$ a$^{-1}$ and 10.92 Mg C ha$^{-1}$ a$^{-1}$, respectively, for boreal, temperate and tropical forests [2]. The mean annual soil CO$_2$ efflux of Chinese subtropical forests is 10.64 Mg C ha$^{-1}$ a$^{-1}$, which is comparable to the reported value from global tropical forests [2]. In the current subtropical forest stand, annual $R_s$ emission (7.93 Mg C ha$^{-1}$ a$^{-1}$) is similar to the value reported in the tropical and subtropical forests (3.45–15.2 Mg C ha$^{-1}$ a$^{-1}$) [20]. Annual $R_s$ efflux in *Michelia wilsonii* forest is higher than those of *Cunninghamia lanceolata* plantation in Hunan (4.55 Mg C ha$^{-1}$ a$^{-1}$) and Fujian (4.54 Mg C ha$^{-1}$ a$^{-1}$) of eastern subtropical China [21, 22], and is comparable to those of *Castanopsis kawakamii* forest (9.34 Mg C ha$^{-1}$ a$^{-1}$) and *Pinus massoniana* forest (9.57 Mg C ha$^{-1}$ a$^{-1}$) [23], but is lower than those of *Mytilaria laosensis* (10.68 Mg C ha$^{-1}$ a$^{-1}$), and *Castanopsis carlesii* (11.18–12.31 Mg C ha$^{-1}$ a$^{-1}$) and *Cunninghamia lanceolata* forests (11.99 Mg C ha$^{-1}$ a$^{-1}$) in subtropical China [9, 22, 24, 25]. These differences may be attributed to climates, vegetation types or substrate quality. Previous studies suggested that mean annual temperature (MAT) and mean annual precipitation (MAP) were positively correlated with $R_s$ [4]. Additionally, there is also a positive relationship ($R^2 = 0.35$, $P = 0.02$) between annual respiration flux and MAT in Chinese subtropical forest ecosystems, expect for the Mt. Ailao forest site (S1 Fig; S1 Table). Similarly, annual respiration flux is significantly positively correlated with MAP ($R^2 = 0.31$, $P = 0.03$) in subtropical China. In our site, both MAT (15.2˚C) and MAP (1 243 mm) were lower than those reported in Fujian (MAT 20.1˚C and MAP 1 670 mm) [24] and in Jiangxi (MAT 17.9˚C and MAP 1 469 mm) [16], respectively. As a result, lower MAT and MAP may, to some extent, account for our smaller annual $R_s$ flux as compared to other subtropical forests with higher MAT and MAP.

**Contribution of components to total soil respiration**

The relative contributions of $R_A$ and $R_H$ to total $R_s$ varied with forest types, climate and methods [26–29]. $R_A$ contributed 14%-73% to $R_s$ among global forest ecosystems [27]. Likewise,
The $R_{H}/R_S$ varied from 10% to 94% among global forest ecosystems [4]. A global synthesis of forest soil respiration showed that the contribution of $R_A$ to total $R_S$ is higher in deciduous broadleaf forest than in evergreen broadleaf forest and evergreen needle leaf forest [4]. For example in a temperate deciduous forest in northern China, the higher $R_A/R_S$ (ranged from 61.7%–77%) is closely related to the higher root biomass associated with belowground carbon metabolisms [30]. In this case, mean $R_A/R_S$ was 41.1%, which was higher than the mean value (30%) of global forest ecosystems [2]. Similarly, the mean $R_A/R_S$ value (41.1%) estimated in this evergreen broad-leaved forest is comparable to the results observed in a monsoon evergreen broad-leaved forest (tree species name) (44.52%) in southern China [31], but is lower than the findings investigated in an evergreen needle forest (Pinus massoniana) (55–63%) or in a deciduous broadleaf forest (tree species name) (54–59%) [32]. As a consequence, the contribution of $R_A$ to $R_S$ might, to large extent, be dependent on forest functional type that determines the belowground root growth and activities [11, 30–32].

Additionally, in this study, the relative contribution of $R_A$ and $R_H$ to $R_S$ largely varied with season. Over the growing seasons (from July to August) of two years, $R_A$ contributed more to $R_S$ as compared to $R_H$. This is due to the fact that $R_A$ and $R_H$ are dominated by different mechanisms [10]. $R_A$ is closely linked to root activity and photosynthesis, while $R_H$ is the respiratory product of soil organic matter decomposition that mainly controlled by substrate and temperature [26]. As a result, there is a significant increase in $R_A$ during the growing seasons in M. wilsonii forest as a result of fast root growth and large root secretions. In addition, $R_H/R_A$ increased with soil temperature but $R_A/R_A$ decreased with soil temperature. $R_A$ was more sensitive to temperature relative to $R_H$. Such results also can, to some extent, account for the higher $R_H/R_A$ in the growing season noted in this study.

Litter respiration is an important source of CO₂ emission. In our study, annual CO₂ emission from litter layer was 2.61 Mg C ha⁻¹ a⁻¹, which value is higher than the results observed in Cunninghamia lanceolata (1.15 Mg C ha⁻¹ a⁻¹) and Castanopsis kawakamii (1.17 Mg C ha⁻¹ a⁻¹) forests in subtropical China [5, 22], but is lower than the values reported in a Castanopsis carlesii forest (4.34 Mg C ha⁻¹ a⁻¹) [5], indicating $R_L$ is mainly regulated by tree-associated litter quantity and quality [8]. During the experimental period, aboveground litter accounted for 14.1%–67.5% of total $R_S$, with a mean value of 32.9%, which is close to the results found in secondary Castanopsis carlesii forest (34.4%) [5]. Numerous studies have evidenced that litter manipulation could markedly change total soil respiration [5, 8, 33]. Li et al. [5] found that
litter addition could enhance annual CO$_2$ flux by approximately 12.5%, but decreased by 15.1% when the litter was removed.

**Temperature sensitivity of soil respiration components**

Over past decades, the temperature sensitivity of $R_S$ (hereafter referred to as apparent temperature sensitivity) has gained more attention due to its importance for climate-carbon feedback in terrestrial ecosystems. In this study, the temperature sensitivity ($Q_{10}$ value) of $R_S$ was 2.01, which is similar to the mean value (2.51) of Chinese forest ecosystems [12], but is lower than
the mean value (3.4) estimated for global forest ecosystems [4]. Different components of $R_S$ may response to soil temperature differently [34]. For an example, the $Q_{10}$ value for $R_A$ and $R_H$ was 3.74 and 1.92 in a Castanopsis carlesii plantation, respectively [24]. A synthesis also indicated that the $Q_{10}$ value of $R_A$ is significantly higher than that of $R_H$ in global forest ecosystems [4]. Similarly, the $Q_{10}$ value of $R_A$ and $R_H$ was 4.01 and 1.34, respectively in the present study, implying that $R_A$ is more temperature-dependent as compared to $R_H$. The C release derived from litter layer is easier to be affected precipitation as compared to $R_A$ and $R_H$. There was a negative relationship between $R_L$ and soil moisture in this study. Thus, the temperature dependence of $R_L$ could, to large extent, be offset and complicated by negative effect of soil moisture. Therefore, no significant correlation was detected between $R_L$ and soil temperature in the present study. A significant positive linear correlation was found between $R_A/R_H$ and $Q_{10}$ of $R_A$ in Chinese subtropical forests ($R^2 = 0.72, P < 0.01, S2$ Fig). Such result showed that a greater

Fig 5. A path analysis model of the relationships among the monthly flux of soil respiration fractions, and environmental variables and litterfall in the $Michelia wilsonii$ plantation of southwestern China. $T_{air}$: monthly mean air temperature, $T_{soil}$: monthly mean soil temperature, Rainfall: monthly rainfall amount, Litterfall: monthly aboveground litter production, Moisture: soil moisture. Solid lines are shown positive correlations path, dashed lines are shown negative paths, and gray lines mean removal paths. Standardized coefficients are listed on each path. ** mean significant difference at 0.05 level, *** mean significant difference at 0.01 level, **** mean significant difference at 0.001 level.

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contribution of \( R_A \) to \( R_S \) may produce a higher \( Q_{10} \) of \( R_A \), suggesting that root activities might more sensitive to future warming [4].

**Effects of environmental factors on soil respiration components**

\( R_A \) is mainly influenced by tree species and root activity [14]. However, both \( R_{H} \) and \( R_{L} \) are mainly influenced by soil temperature and substrate properties. The path analysis indicated that measured variables together explained 82% and 87% variations monthly fluxes of \( R_S \) and \( R_A \), respectively (Fig 5A and 5B). Soil temperature is a key factor regulating the variations of two components. Contrastingly, all factors together only accounted for 43% variations in monthly flux of \( R_{H} \). This is attributed to the fact that season-associated changes, such as moisture or microbes, counteract the dominant effect of temperature on \( R_{H} \). Similar phenomena have recently been observed in grassland ecosystem [35].

Similar to \( R_{H} \), litter layer is stored on the surface of the forest ground. The CO\(_2\) emission from litter decomposition is easy to be affected directly and/or indirectly by multiple factors, including temperature, moisture, microorganisms. Path analysis showed that all factors together only explained 35% variation in monthly flux of \( R_{L} \). Sufficient soil moisture associated with frequent rainfall in the study area throughout the year may overshadow temperature effect [36]. A recent study also suggested that soil temperature had no significant impacts on \( R_{L} \) in a subtropical mixed forest [37].

Trees species-induced variation in the quantity and quality of litterfall might impact the relationship between \( R_{L} \) and litterfall [17]. For an instance, there was a significant relationship between \( R_{L} \) and litter mass of the current month in *Cunninghamia lanceolata* forest. However, \( R_{L} \) was significantly related to the litterfall of two months ago in *Castanopsis carlesii* forest [5]. In our site, *M. wilsonii* is a broad-leaved evergreen tree species, whose litterfall had a peak in winter and a sub-peak in spring. Several results have suggested a potentially lagged effect of litterfall on \( R_{L} \) in subtropical forests [5, 17]. Similar finding was observed in our study. There was a significant correlation between \( R_{L} \) rate (4 months behind) and monthly litterfall in the *M. wilsonii* forest (\( R^2 = 0.46, P = 0.04 \)).

**Conclusions**

We separated \( R_S \) into different components (\( R_A, R_{H} \) and \( R_{L} \)) using trenching and litter removal techniques in a subtropical *M. wilsonii* forest of southwestern China. The contribution of each component to total \( R_S \) varied with seasons. \( R_A/R_S \) increased with increasing soil temperature, whilst both \( R_{H}/R_S \) and \( R_{L}/R_S \) declined with increasing soil temperature. Path analysis showed that monthly fluxes of each component were dominated by different factors. \( T_{soil} \) and other factors can well-predict the seasonal dynamics of \( R_S \) and \( R_A \). Measured variables did not show a good correlation with \( R_{H} \) and \( R_{L} \). The results noted in this study highlight the important implication of rainfall and root phenology for soil respiration in subtropical forests in this specific region.

**Supporting information**

S1 Fig. \( R_S \) responded non-linearly to MAT (a), but responded linearly to MAP (b) in subtropical forests of China. Open circle represents outlier result and was obtained from the Mt. Ailao subtropical forest data, which was not included in the regression. (DOCX)

S2 Fig. \( Q_{10} \) of \( R_A \) was positively correlated with \( R_A/R_S \). (DOCX)
S1 Table. Values of forest CO₂ efflux from partial Chinese subtropical forests in literature. (DOCX)

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References
1. Schimel D, Melillo J, Tian H, McGuire AD, Kicklighter D, Kittel T, et al. Contribution of increasing CO₂ and climate to carbon storage by ecosystems in the United States. Science. 2000; 287: 2004–2006. PMID: 10720324
2. Raich JW, Schlesinger WH. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus. 1992; 44B: 81–99.
3. Davidson EA, Janssens IA. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature. 2006; 440: 165–173. https://doi.org/10.1038/nature04514 PMID: 16525463
4. Wang W, Chen WL, Wang SP. Forest soil respiration and its heterotrophic and autotrophic components: Global patterns and responses to temperature and precipitation. Soil Biol Biochem. 2010; 42: 1236–1244.
5. Li XJ, Liu XF, Xiong DC, Lin WS, Lin TW, Shi YW, et al. Impact of litterfall addition and exclusion on soil respiration in Cunninghamia lanceolata plantation and secondary Castanopsis carlesii forest in mid-subtropical China. Chin J Plant Ecol. 2016; 40: 447–457.
6. Chen X, Chen HYH. Global effects of plant litter alterations on soil CO₂ to the atmosphere. Global Change Biol. 2018; 24: 3462–3471.
7. Bowden RD, Nadelhoffer KJ, Boone RD, Melillo JM, Garrison JB. Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. Can J For Res. 1993; 23: 1402–1407.
8. Sulzman EW, Brant JB, Bowden RD, Lajtha K. Contribution of aboveground litter, belowground litter, and rhizosphere respiration to total soil CO₂ efflux in an old growth coniferous forest. Biogeochemistry. 2005; 73: 231–256.
9. Li W, Liu XF, Chen GS, Zhao BJ, Qiu X, Yang YS. Effects of litter manipulation on soil respiration in the natural forests and plantations of Castanopsis carlesii in mid-subtropical China. Sci Silvae Sin. 2016; 52: 11–18.
10. Yu SQ, Chen YQ, Zhao J, Fu SL, Li ZA, Xia HP, et al. Temperature sensitivity of total soil respiration and its heterotrophic and autotrophic components in six vegetation types of subtropical China. Sci Total Environ. 2017; 607–608: 160–167.
11. Vargas R, Allen MF. Environmental controls and the influence of vegetation type, fine roots and rhizomorphs on diel and seasonal variation in soil respiration. New Phytol. 2008; 179: 460–471. PMID: 19086292
12. Xu ZF, Tang SS, Xiong L, Yang WQ, Yin HJ, Tu LH, et al. Temperature sensitivity of soil respiration in China's forest ecosystems: Patterns and controls. Appl Soil Ecol. 2015; 93: 105–110.

13. Davidson EA, Belk E, Boone RD. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Global Change Biol. 1998; 4: 217–227.

14. Rey A, Pegoraro E, Tedeschi V, De Parri I, Jarvis PG, Valentini R. Annual variation in soil respiration and its components in a coppice oak forest in Central Italy. Global Change Biol. 2002; 8: 851–866.

15. Chen GS, Yang YS, Wang XG, Xie JS, Gao R, Li Z. Root respiration in a natural forest and two plantations in subtropical China: seasonal dynamics and controlling factors. Acta Ecol Sin. 2005; 25: 1941–1947.

16. Wang YD, Wang HM, Xu MJ, Ma ZQ, Wang ZL. Soil organic carbon stocks and CO$_2$ effluxes of native and exotic pine plantations in subtropical China. Catena. 2015; 128: 167–173.

17. Huang ZQ, Yu ZP, Wang MH. Environmental controls and the influence of tree species on temporal variation in soil respiration in subtropical China. Plant Soil. 2014; 382: 75–87.

18. Sheng H, Yang YS, Yang ZJ, Chen GS, Xie JS, Guo JF, et al. The dynamic response of soil respiration to land-use changes in subtropical China. Global Change Biol. 2010; 16: 1107–1121.

19. Xu ZF, Zhou FF, Yin HJ, Liu Q. Winter soil CO$_2$ efflux in two contrasting forest ecosystems on the eastern Tibetan Plateau, China. J For Res. 2015; 26: 679–686.

20. Raich J.W, Potter C.S. Global patterns of carbon dioxide emissions from soils. Global Biogeochem Cycles. 1995; 9: 23–36.

21. Tian DL, Wang GJ, Peng YY, Yan WD, Fang X, Zhu F, et al. Contribution of autotrophic and heterotrophic respiration to soil CO$_2$ efflux in Chinese fir plantations. Aust J Bot. 2011; 59: 26–31.

22. Yang YS, Chen GS, Guo JF, Xie JS, Wang XG. Soil respiration and carbon balance in a subtropical native forest and two managed plantations. Plant Ecol. 2007; 193: 71–84.

23. Zhang R, Bai Y, Liu J, Jiang PK, Zhou GM, Wu JS, et al. Effects of conversion of natural broad-leaved forest to Chinese fir plantation on soil respiration in subtropical China. Chin J Appl Ecol. 2015; 26: 2946–2952.

24. Wu JJ, Yang ZJ, Liu XF, Xiong DC, Lin WS, Chen CQ, et al. Analysis of soil respiration and components in Castanopsis carlesi and Cunninghamia lanceolata plantations. Chin J Plant Ecol. 2014; 38: 45–53.

25. Yu ZP, Huang ZQ, Wang MH, Hu ZH, Hua WX, Qiang LR, et al. Seasonal Dynamics of Soil respiration and Its Affecting Factors in Subtropical Mytilaria laosensis and Cunninghamia lanceolata Plantations. Sci Silvae Sin. 2014; 50: 7–14.

26. Wangdi N, Mayer M, Nirola MP, Zangmo N, Ahmed IU, et al. Soil CO$_2$ efflux from two mountain forests in the eastern Himalayas, Bhutan: components and controls. Biogeosciences. 2017; 14: 99–110.

27. Subke JA, Inglima I, Cotrufo MF. Trends and methodological impacts in soil CO$_2$ efflux partitioning: A meta-analytical review. Global Change Biol. 2006; 12: 921–943.

28. Huang WJ, Han TF, Liu JX, Wang GS, Zhou GY. Changes in soil respiration components and their specific respiration along three successional forests in the subtropics. Funct Ecol. 2016; 30: 1466–1474.

29. Shi BK, Gao WF, Jin GZ. Effects on rhizospheric and heterotrophic respiration of conversion from primary forest to secondary forest and plantations in northeast China. Eur J Soil Biol. 2015; 66: 11–18.

30. Wang CK, Yang JY. Rhizospheric and heterotrophic components of soil respiration in six Chinese temperate forests. Global Change Biol. 2007; 13: 123–131.

31. Han TF, Zhou GY, Li YL, Liu JX, Zhang DQ. Partitioning soil respiration in lower subtropical forests at different successional stages in southern China. Chin J Plant Ecol. 2011; 35: 946–954.

32. Yi ZG, Fu SL, Yi WM, Zhou GY, Mo JM, Zhang DQ, et al. Partitioning soil respiration of subtropical forests with different successional stages in south China. For Ecol Manage. 2007, 243: 178–186.

33. Tan ZH, Zhang YP, Liang NS, Song QH, Liu YH, You G, et al. Soil respiration in an old-growth subtropical forest: Patterns, components, and controls. J Geophys Res: Atmos. 2013; 118: 2981–2990.

34. Butler A, Meir P, Saiz G, Maracahipes L, Marimon BS, Grace J. Annual variation in soil respiration and its component parts in two structurally contrasting woody savannas in Central Brazil. Plant soil. 2012; 352: 129–142.

35. Moinet GYK, Cieraad E, Hunt JE, Fraser A, Turnbull MH, Whitehead D. Soil heterotrophic respiration is insensitive to changes in soil water content but related to microbial access to organic matter. Geoderma. 2016; 274: 68–78.

36. Tu LH, Hu TX, Zhang J, Li XW, Hu HL, Liu L, et al. Nitrogen addition stimulates different components of soil respiration in a subtropical bamboo ecosystem. Soil Biol Biochem. 2013; 58: 255–264.
37. Yu L, Wang YJ, Wang YQ, Sun SQ, Liu LZY. Quantifying components of soil respiration and their response to abiotic factors in two typical subtropical forest stands, southwest China. PloS One. 2015; 10, e0117490. https://doi.org/10.1371/journal.pone.0117490 PMID: 25680112