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Characteristics of Soil Respiration and Its Components of a Mixed Dipterocarp Forest in China

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Academic Editor: Megan E. McGroddy

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Abstract: Background: Although numerous studies have been carried out in recent decades, soil respiration remains one of the less understood elements in global carbon budget research. Tropical forests store a considerable amount of carbon, and a well-established knowledge of the patterns, components, and controls of soil respiration in these forests will be crucial in global change research. Methods: Soil respiration was separated into two components using the trenching method. Each component was measured at multiple temporal scales and in different microhabitats. A commercial soil efflux system (Li8100/8150) was used to accomplish soil respiration monitoring. Four commonly used models were compared that described the temperature dependence of soil heterotrophic respiration using nonlinear statistics. Results and Conclusions: Trenching has a limited effect on soil temperature but considerably affects soil water content due to the exclusion of water loss via tree transpiration. Soil respiration decreased gradually from 8 to 4 $\mu mol \cdot m^{-2} \cdot s^{-1}$ 6 days after trenching. Soil autotrophic (R_a) and heterotrophic respiration (R_h) have contrasting diel patterns and different responses to temperature. R_h was negatively correlated with temperature but positively correlated with relative humidity. Both R_a and R_h varied dramatically among microhabitats. The Q_{10} value of R_h derived using the Q_{10} model was 2.54. The Kirschbaum–O'Connell model, which implied a strong decrease of Q_{10} with temperature, worked best in describing temperature dependence of R_h. Heterotrophic respiration accounted for nearly half of the total soil efflux. We found an unexpected diurnal pattern in soil heterotrophic respiration which might be related to diurnal moisture dynamics. Temperature, but not soil moisture, was the major controller of seasonal variation of soil respiration in both autotrophic and heterotrophic components. From a statistical perspective, the best model to describe the temperature sensitivity of soil respiration was the Kirschbaum–O'Connell model. Soil respiration varied strongly among the microhabitats and played a crucial role in stand-level ecosystem carbon balance assessment.

Keywords: microhabitat; diurnal pattern; temperature sensitivity; moisture; carbon sink

1. Introduction

Soil respiration is an important process in carbon cycle of terrestrial ecosystems. Numerous studies have been carried out to investigate topics of soil respiration or efflux, from tropical to boreal forests [1,2]. However, current knowledge on soil respiration is still poor compared to that on photosynthesis. It is necessary to achieve a process-based model on soil respiration which is similar to photosynthesis biochemical models [3].

Tropical forest, where a warm and wet climate drives fast biogeochemical turnover, plays a major role in global carbon cycling and, hence, the rate of climatic warming [4].

Nevertheless, soil respiration studies on tropical forests are much fewer in number than those on boreal or temperate forests [5–7]. In the tropical forests near the equator, the annual temperature range is small compared to boreal or temperate forests. The common temperature dependence of soil respiration in other biomes was not detected in these equatorial tropical forests [8,9]. Even in the case of tropical seasonal forests, soil respiration was found not related to temperature [10–12]. This hindered the assessment of temperature sensitivity in tropical soil respiration, an important parameter in climatic and biogeochemical models.

Soil respiration is the sum of autotrophic respiration by plant roots and heterotrophic respiration by soil microbes. Since different organisms are involved in these two componential processes, they might respond differently to environmental changes. Thus, it is necessary to separate them when carrying out soil respiration studies. However, such steps have seldom been taken in previous studies on tropical soil respiration.

To investigate the pattern, components, and controls of tropical forest soil respiration, we used the trenching method and measured the two componential processes of soil respiration in a mixed dipterocarp forest in China. The specific aims of the study were (1) to determine temperature sensitivity and the best model describing this sensitivity, (2) to separate respiration into autotrophic and heterotrophic components, as well as investigate their patterns and controls, and (3) to investigate how soil respiration varies among microhabitats. In the mixed dipterocarp forest, the annual temperature range could be up to 10 °C; thus, it was feasible to achieve our objects in our study site.

2. Materials and Methods

2.1. Site Description

The experiment was carried out in a dipterocarp forest on the northern edge of tropical Southeast Asia, in Xishuangbanna, China, at 21°37′ N, 101°35′ E [13]. The climate of this area shows strong seasonality. A local meteorologist divided the whole year into three sub-seasons: the dry hot season (March and April), fog cool season (November through February next year), and rainy season (May through October) [14]. Climatic records over the past 50 years showed a mean annual total rainfall of about 1500 mm, 87% of which occurred in the rainy season. The remaining 13% (195 mm) occurred in the dry half of the year, when the monthly rainfall was usually less than 50 mm. Mean annual air temperature is around 21.8 °C, while the coldest monthly mean temperature is below 15 °C and cold fronts can lower the temperature to 2–4 °C.

The forest being studied here is a primary mixed dipterocarp forest, referred to by local vegetation scientists as a tropical seasonal rainforest (Figure 1). This forest is famous for its particularly tall trees which can reach heights of 60–70 m. The forest canopy is very complex with multiple layers. A closed canopy exists at 25–35 m, while emergent trees (mostly *Shorea wantianshuea*) reach 60–70 m. The mean diameter at breast height is 5.69 cm, and the mean total basal area for trees with a diameter at breast height above 1.0 cm is 42.34 m^2 per hectare. The mean stand biomass is 421 t of dry matter per hectare, which is close to the biomass levels in equatorial rainforest in Pasoh [13,15]. The presence of large logs, many epiphytes, an uneven age distribution, and complex canopy characterizes the forest as "old growth". The soil is lateritic, derived from siliceous rocks such as granite and gneiss, with pH from 4.91, and the organic matter content of the 0–20 cm mineral soil layer is approximately 20 g·kg^{-1}. [15]. A 20 ha permanent plot was established in 2007 for the purpose of studying the structure and dynamics of the dipterocarp forest.
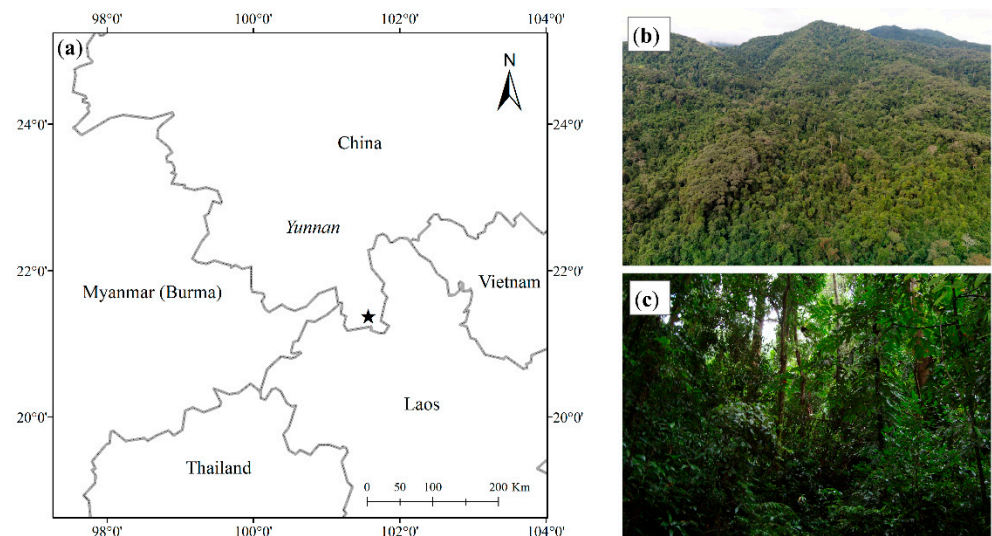
Figure 1. Site location (★) and the landscape: (**a**) site location; (**b**) canopy; (**c**) understory.

2.2. Experimental Design

The studied forest is located in a mountainous area [13] (cf. Figure 2 in terrain map), and the terrain is very complex (Figure 1). The elevation gradient of this area varies from 709 to 869 m above sea level. Different microhabitats exist due to changes in micro-terrain. It is noted that forest soil respiration has strong spatial heterogeneity, and the degree of variation could be enforced by the complex micro-terrain [15]. Taking representative measurements in this area is a challenging task, and each microhabitat should be considered.
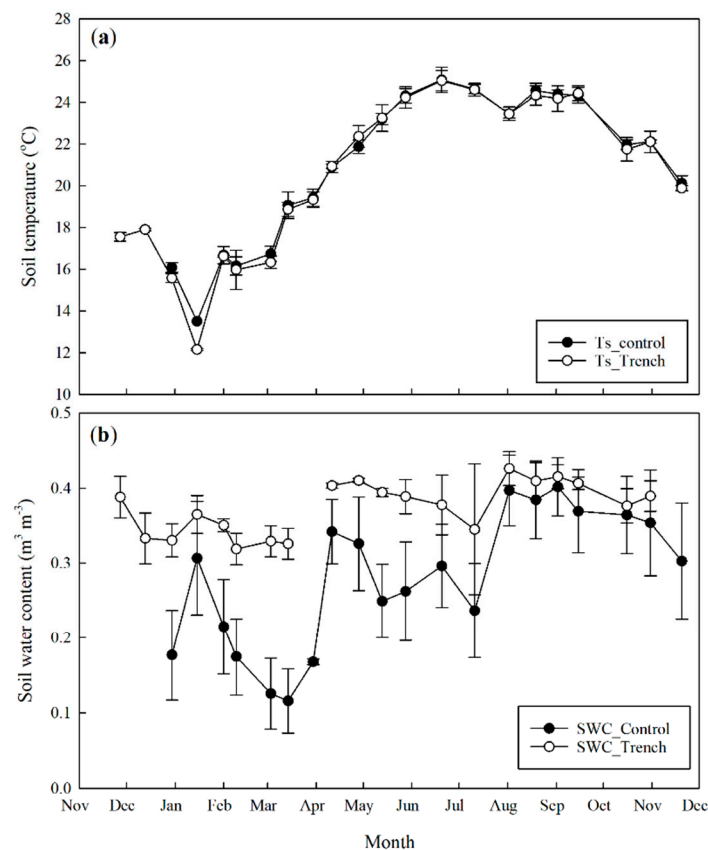
Figure 2. Temporal dynamics of soil temperature (**a**) and soil water content (**b**). Both soil temperature and soil water content were measured at a depth of 5 cm. Error bars represent standard deviation.

We firstly chose a small low-elevation hill as the target site for soil respiration in this study. The small hill has an area of around 60×50 m and is irregular in shape. The slope is gentle (around 6–15 degree) in this small hill. Below the hill is a watershed stream and a small pond. We chose this small low-elevation hill as the study site, considering the representativeness of this site and the difficulties in placing soil respiration instruments, here the Li-8150, at sites with steep slopes.

The small hill was classified into the following three microhabitats: (1) forest gap (Plot #1); (2) upper slope (Plot #2); (3) lower slope valley (Plot #3). There is a new forest gap in the lower-slope position of the target hill; thus, we set up Plot #1 near this gap. The upper-slope microhabitat (Plot #2) has little organic litter on the floor as the runoff flow of rain could drive the litter and nutrients to the lower habitats. Thus, it could be viewed as a nutrient- and organic-poor habitat. The lower-slope habitat, on the contrary, has a relatively thick decaying litter, and the soil surface looks darker than that of the upper-slope habitat.

In each microhabitat, we set up two paired plots. One plot was trenched, and the paired plot within the same habitat was treated as a control. The plot was 3×3 m in size. The 50 cm wide trench had a depth of 120–130 cm. The trench was refilled with the excavated soil. In order to avoid root growth into the plot, four high-quality plexiglass sheets were erected in the trench of each plot. We believed that this trench depth could cut off all roots in this study forest, as no roots were visible at this depth. Soil was hard and rock was semi-weathered at this depth. In the center of each plot, we randomly placed 3–4 collars for soil measurements.

2.3. Measurements of Soil Respiration and Microclimatic Factors

A commercial soil efflux system was used to measure soil respiration and microclimatic factors. Some of the self-made soil efflux chambers used fans to mix air in the chamber during measurement. However, it has been experimentally established that soil efflux rates increase linearly with wind speed [16]. The Li-8100/8150 multiplexer automatic soil CO_2 flux system (Li-Cor Inc, Lincoln, NE, USA) selected for this study has a special design that avoids the use of fans during measurement [17].

The Li-8150, connected with eight chambers, was used three times. The first time was to monitor how soil respiration changed during and after trenching. The second and third times were to monitor diurnal variation during the dry and rainy seasons. The second measurement ran from 22 March 2015 to 29 March 2015. Data from the third set of measurements were not used here for experimental reasons. Air relative humidity data were collected from a nearby tower in the same time period.

The Li-8100 was used to carry out regular soil respiration measurements twice a month for detecting seasonal patterns and for annual sum estimation. Each time, soil respiration measurements were started at 11:00 a.m. and lasted until 1:00 p.m. Each collar was measured three times. Soil water content (S_{WC}) and soil temperature (T_s) were measured at the same time with sensors provided by the manufacturers.

2.4. Definition and Calculations

The commercial efflux system provides calculated soil carbon dioxide flux by either linear or exponential fitting of the CO_2 concentration to time (cf. Li-Cor 8100/8150 manual). We did not carry out further recalculations but adopted the values generated by the system. Soil carbon dioxide flux measured in the control and trench treatment were regarded as total soil respiration (R_s) and heterotrophic respiration (R_h), respectively. Autotrophic respiration (R_a) was calculated as the difference between R_s and R_h. The annual sum of respiration was extrapolated by integrating with time.

2.5. Models for Temperature Response of Soil Respiration

There are four commonly used models in describing temperature dependence of soil heterotrophic respiration (R_h):

$$R_h = R_{10}Q_{10}^{[(T-10)/10]}, \ Q_{10} \text{ model}, \tag{1}$$

$$R_h = R_{10}\exp[\frac{E_a}{R}(\frac{1}{10+273.15} - \frac{1}{T+273.15})], \ \text{Arrhenius model}, \tag{2}$$

$$R_h = \alpha\exp[E_0(\frac{1}{283.15 - T_0} - \frac{1}{T_K - T_0})], \ \text{Lloyd–Kavanau model}, \tag{3}$$

$$R_h = \alpha\exp[\beta T(1 - 0.5\frac{T}{T_m})], \ \text{Kirschbaum–O׳Connell model}, \tag{4}$$

where R_{10} is the reference respiration at 10 °C, T is the driving temperature, T_K is the driving temperature in units of Kelvin, Q_{10} is the temperature sensitivity index defined as $Q_{10} = \frac{R_h(T+10)}{R_h(T)}$, E_a is the activation energy, R is the gas constant (8.314 J·mol^{-1}·K^{-1}), α, β, and T_m are fitted parameters, E_0 is a similar but loose term of activation energy $E_0 \approx \frac{E_a}{RT_K}$, and T_0 is a fitted parameter, the initial value of which needs to be lower than any observed temperature when applying nonlinear regression.

The Q_{10} expression for each model is as follows:

$$Q_{10} \text{ model}: \ Q_{10} = Cons, \tag{5}$$

$$\text{Arrhenius model}: \ Q_{10} = \exp(\frac{10E_a}{RT(T+10)}), \tag{6}$$

$$\text{Lloyd–Kavanau model}: \ Q_{10} = \exp(\frac{10E_0}{(T-T_0)(T+10-T_0)}), \tag{7}$$

$$\text{Kirschbaum–O׳Connell model}: \ Q_{10} = \exp(10\beta(1 - \frac{T}{T_m}) - \frac{50\beta}{T_m}), \tag{8}$$

where *Cons* indicates a constant.

All nonlinear regressions in the study were performed using Matlab 7.1 (Mathworks Inc., Natick, MA, USA). We used the determinant coefficient (r^2) and sum of residual squares (SSR) to assess goodness of fit. The upper and lower 95% confidential intervals of each fitted parameter were provided.

3. Results

3.1. Trench Effect on Soil Microclimate and Soil Respiration

Trenching had a limited effect on soil temperature (T_s). There was no difference in T_s between control and trenching treatments (Figure 2a). On the contrary, the effect of trenching on soil water content (S_{WC}) was very strong (Figure 2b). The S_{WC} did not drop even during the driest period in trenching plots.

The effect of trenching on soil respiration was obvious (Figure 3). Average R_s decreased from 8 μmol·m^{-2}·s^{-1} to 4 μmol·m^{-2}·s^{-1} after trenching. This decrease was a gradual process lasting several days.

3.2. Diel Variation of Soil Respiration and Its Components

There were clear diel patterns in soil respiration and its components (Figure 4). Heterotrophic respiration (R_h) decreased from the highest level in the early morning to the lowest level in the late afternoon during the daytime, and then it increased to the highest level in the early morning during the nighttime. This pattern was similar to the pattern of relative humidity (H_r), but not to that of soil temperature (T_s) (Figure 4d). A significant positive correlation was found between R_h and H_r ($r = 0.69$, $p < 0.001$), whereas a significant negative correlation was found between R_h and T_s ($r = -0.64$, $p < 0.001$).
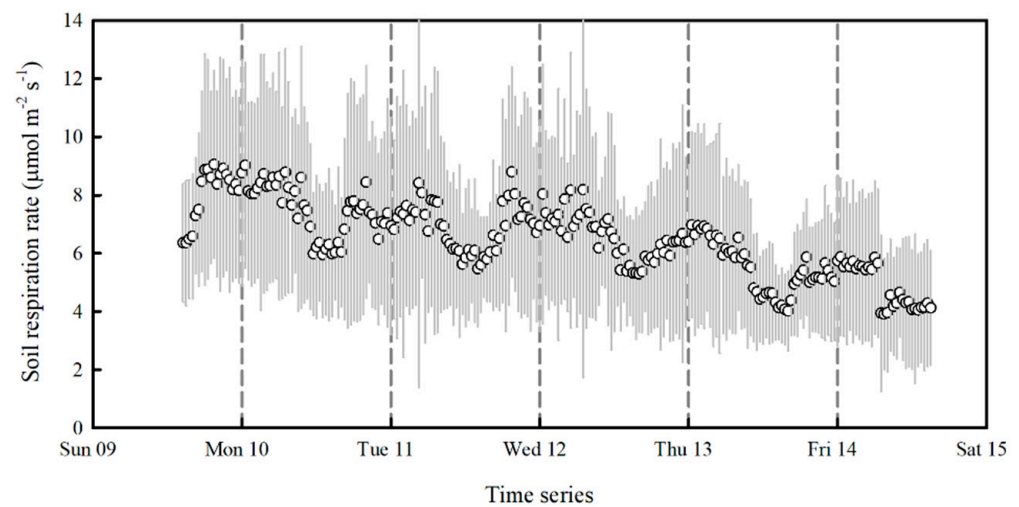
Figure 3. A continuous monitoring of soil respiration rate to show the effect of trenching. Gray shading indicates the standard deviation.
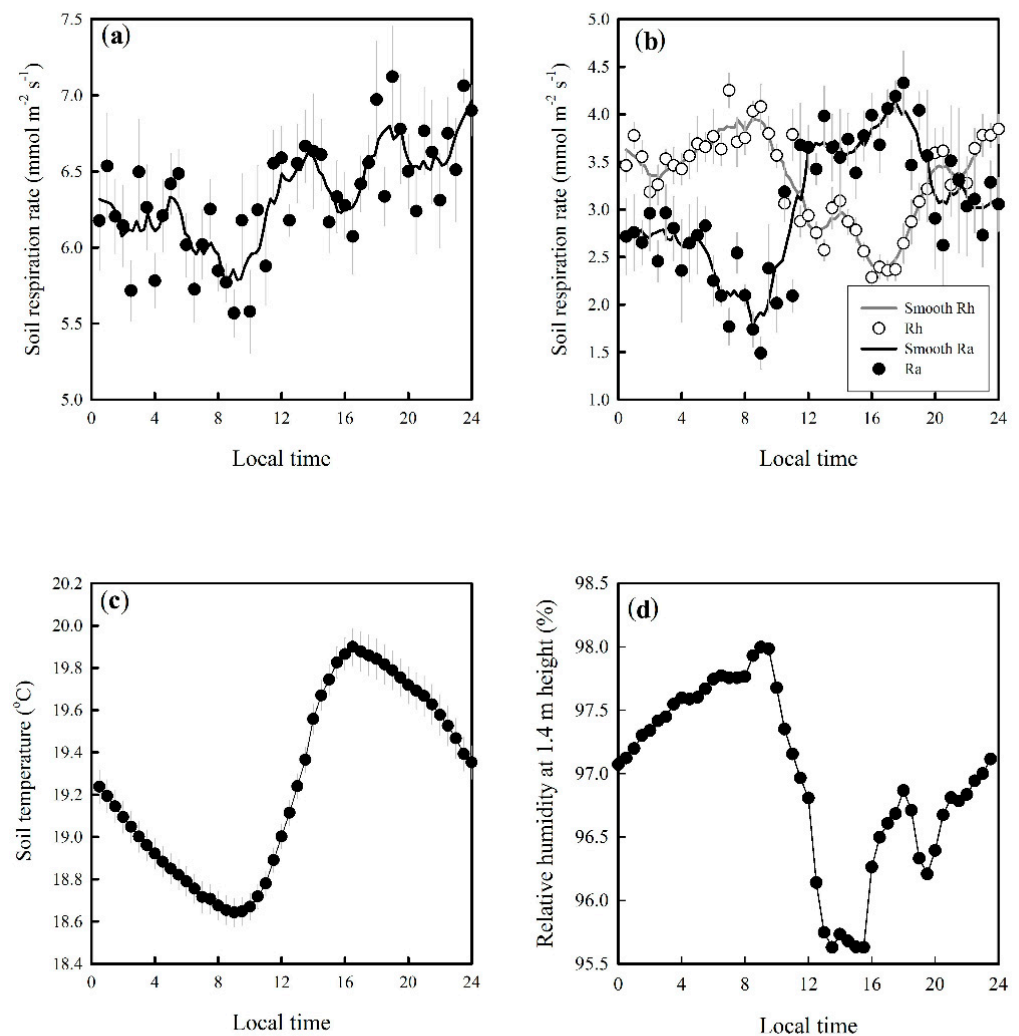

Figure 4. The diurnal variation of soil respiration (**a**), its components (**b**), soil temperature (**c**), and relative humidity of air at 1.4 m height (**d**). R_h: heterotrophic respiration in the trenching treatment; R_a: autotrophic respiration calculated as the difference between total soil respiration and R_h. Error bars indicate the standard deviation.

Autotrophic respiration (R_a) exhibited an opposite diel pattern to that of R_h. R_a was highest in the late afternoon. There was a continuous decrease in R_a during the nighttime. A significant positive correlation was found between R_a and T_s ($r = 0.77$, $p < 0.001$). The diurnal range of R_a (~3 μmol·m^{-2}·s^{-1}) was higher than that of R_h (~1.5 μmol·m^{-2}·s^{-1}). Total soil respiration (R_s) exhibited a similar pattern to that of R_h and was significantly correlated to T_s ($r = 0.58$, $p < 0.001$).

### 3.3. Variation in Soil Respiration across Seasons and Microhabitats

Both R_s and R_h varied dramatically in different microhabitats, with a clear seasonal pattern (Figure 5). The lowest R_s and R_h were observed in the upper-slope microhabitat. The gap plot showed the highest R_s (10.07 ± 3.90 μmol·m^{-2}·s^{-1}). Highest R_h was observed in the lower-slope valley microhabitat (5.27 ± 1.96 μmol·m^{-2}·s^{-1}). The highest R_s values could be as high as three times the lowest values. The R_h in the valley habitat was twice as high as that in the upper-slope habitat.
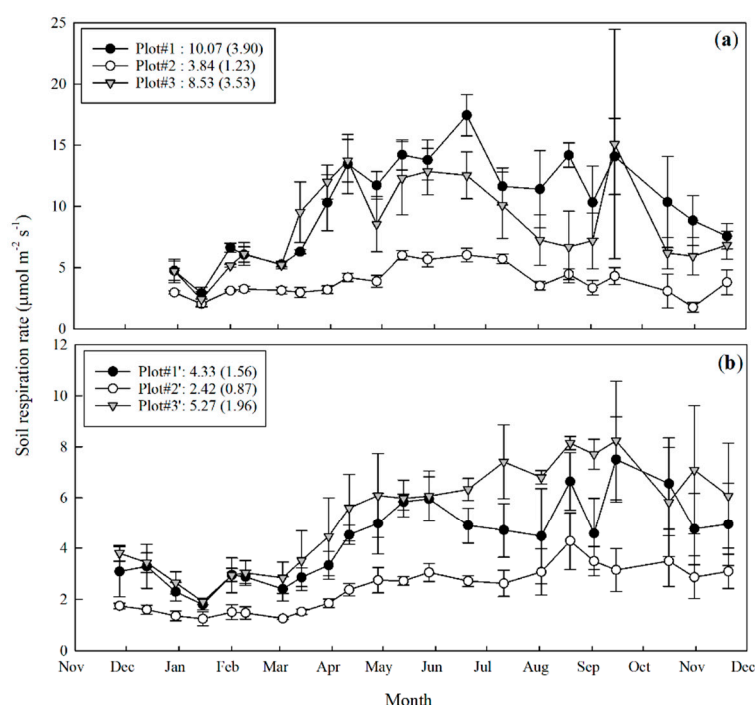
Figure 5. Soil respiration rate of the paired plots in control (**a**) and trenching treatment (**b**). Plot #1 and Plot #1′ are paired plots in forest gap; Plot #2 and Plot #2′ are paired plots in upper slope; Plot #3 and Plot #3′ are paired plots in lower slope valley. Error bars represent the standard deviation.

### 3.4. Temperature Sensitivity of Soil Respiration

Soil respiration, especially the heterotrophic component (R_h), was highly correlated to temperature in the studied forest (Figure 6). The Q_{10} value of R_h derived using the Q_{10} model was 2.54. From a statistical perspective, however, the Q_{10} model did not provide the best description of the temperature dependence of R_h (Table 1). The Kirschbaum–O'Connell model which implied a strong decrease in Q_{10} with temperature fit the best (Figure 7 and Table 1). The Q_{10} values derived using the four models converged at a temperature around 16 °C (Figure 7). The Q_{10} value at the mean annual temperature (22 °C) varied dramatically among models. It was 2.54, 2.40, 1.79, and 1.01 for the Q_{10}, Arrhenius, Lloyd–Kavanau, and Kirschbaum–O'Connell models, respectively.
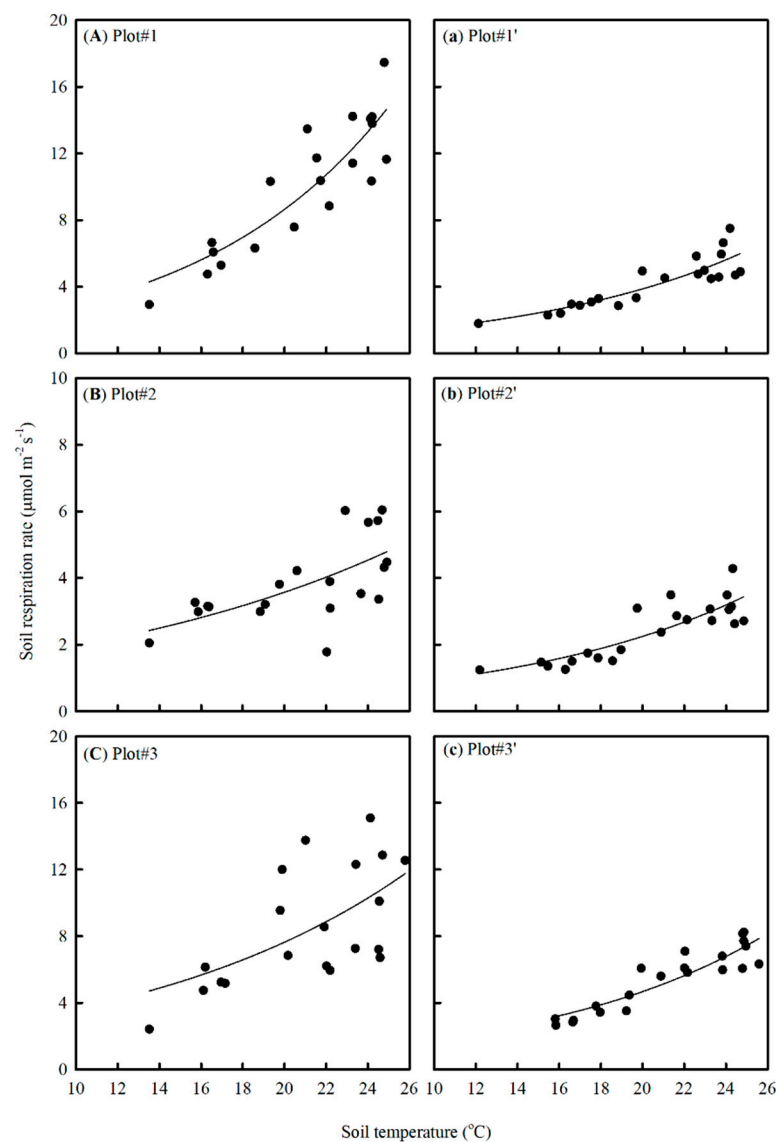
Figure 6. Temperature response of soil respiration rate for the paired plots in different treatments. Plots #1–3 are control treatments; Plots #1′–3′ are trench treatments. Plots #1–3 are paired to Plots #1′–3′ from the forest gap, upper slope, and lower slope valley, respectively. The regression line was fitted using a two-parameter exponential growth equation.

Table 1. Summary table for comparison of the fitting of four models for soil heterotrophic respiration. Values in parentheses are 95% confidential intervals of each estimated parameter; r^2 represents the determinant coefficient; SSE is the sum of squared errors.

Model Type	r^2	SSE	α, R_{10}	Q_{10}, E_a, E_0, β	T_0, T_m
Q_{10}	0.8370	6.8438	1.4254 (1.0161, 1.8347)	2.5474 (1.9729, 3.1219)	
Arrhenius	0.8394	6.7401	1.3761 (0.9718, 1.7803)	65,723 (49,964, 81,481)	
Lloyd–Kavanau	0.8543	6.1016	0.6879 (−0.5530, 1.9289)	50.68 (−97.45, 198.81)	270.20 (237.33, 303.08)
Kirschbaum–O'Connell	0.8643	5.6964	0.0246 (−0.0602, 0.1095)	0.4014 (0.0673, 0.7356)	27.07 (20.20, 33.93)
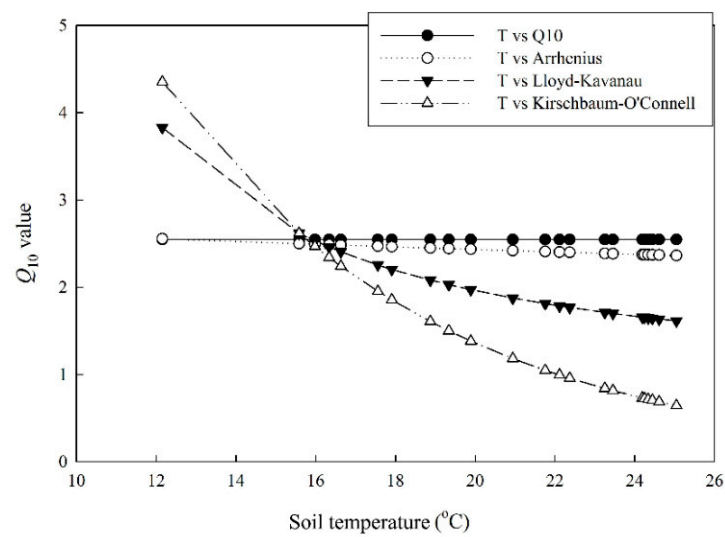
Figure 7. Soil temperature dependence of Q_{10} derived using four different models.

3.5. Contribution of autotrophic and heterotrophic components to total soil respiration

The R_h, R_a, R_s and R_h/R_s all exhibit clear seasonal patterns (Figure 8). In general, R_a and R_s were higher during the rainy season. The R_h, however, increased from the beginning of the rainy season with no obvious decline until the end of the year. The overall mean contribution of R_h to R_s is 57.01%. This implies that the contribution of R_h is slightly higher than that of R_a to R_s.
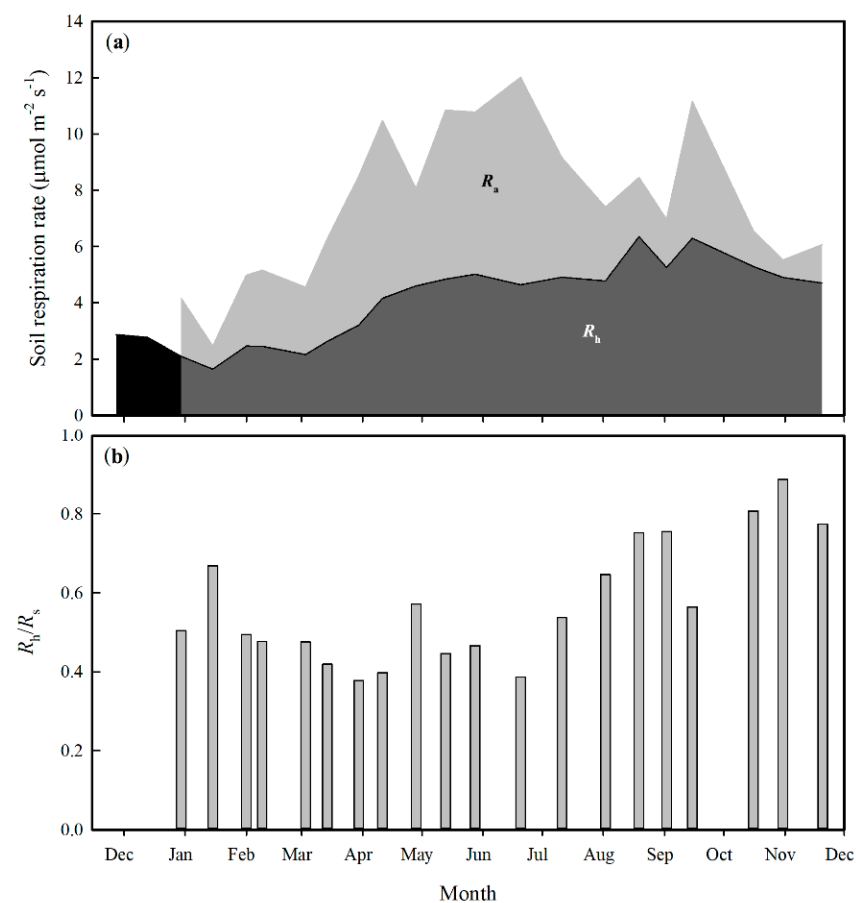

Figure 8. Temporal dynamics of soil respiration rate and its components (**a**), and of R_h/R_s (**b**). R_a: autotrophic respiration, R_h: heterotrophic respiration.

4. Discussion

4.1. The Unexpected Diel Pattern in Heterotrophic Respiration

The effect of trenching on soil temperature was very small, but trenching had an obvious influence on soil water content and soil respiration. This was possibly due to the inhibition of transpiration and consumption of carbohydrates in roots. The existence of a hysteresis between temperature and soil respiration at a diurnal scale has been extensively reported [18]. Nevertheless, the reasons why hysteresis occurs between temperature and R_s are still unknown. In our study, we separated R_s into R_a and R_h using the trenching method and related them to soil temperature (Figure 9). We found contrasting diel patterns in R_h and R_a, as well as in their responses to soil temperature. The diel pattern and its response to soil temperature of R_a were consistent with previous findings [18]. However, the negative correlation between R_h and T_s was unexpected, and, to our knowledge, this is the first report of this new pattern.
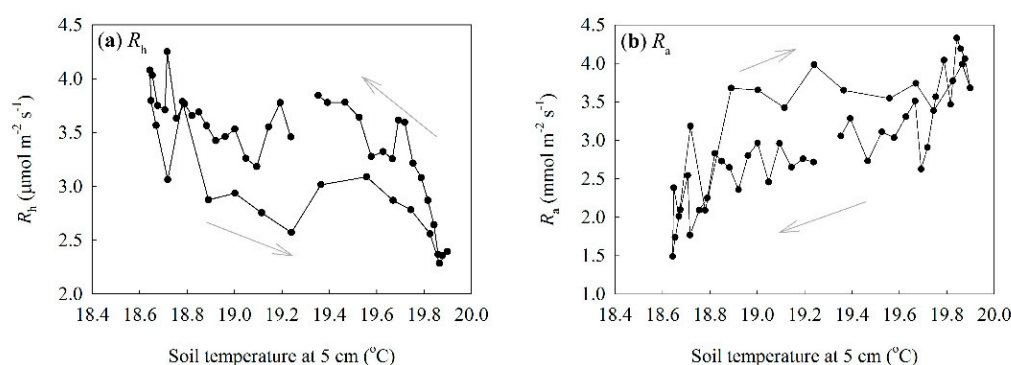
Figure 9. The relationship between soil temperature and soil respiration at diel scale: (**a**) variation of R_h with soil temperature; (**b**) variation of R_a with soil temperature.

We aimed to determine whether this unexpected new diel pattern in R_h is a common pattern or not, and why it occurs. We compared our results with those collected in a tropical secondary forest in Thailand [11]. The lowest R_h occurred after noon [11]. We also compared our results with unpublished data collected in Pasoh, Malaysia (data copyright reserved by Dr. Naishen Liang). The findings from Pasoh showed very similar results to those of this study. We, thus, suspect that this might be a common pattern in tropical forests of Southeast Asia. We further hypothesize that water condition is a major factor leading to the unexpected diel pattern in R_h. The major factors affecting R_h could be summarized as temperature, water, and substrate [19,20]. The substrates for heterotrophic respiration include aboveground (e.g., leaves, branches) and belowground (e.g., dead roots) plant litter and soil organic matter. There is no evidence that these substrates vary significantly from day to night, although they do vary over longer time periods, such as seasonally and annually. Thus, substrate is not likely to account for this pattern. As shown before, there was a negative relationship between R_h and T_s. This violates the basic principle of temperature-driving biochemical processes. Therefore, we could also exclude temperature as the cause for the observed pattern. Thus, the only factor remaining for consideration is water condition.

Evidence in support of the hypothesis that water condition is a major factor leading to the unexpected diel pattern in R_h includes the following:

(i)   We found a close relationship between Rh and relative humidity (Hr).

(ii)   The climate in tropical forests could form a diel dry-and-rewet cycle on surface litter. Evaporation is strong in tropical rainforest because of the high year-round solar radiation and temperature [21,22]. High rates of evaporation dry the air, as well as surfaces of soil litter, during the day. On calm nights, radiation fog can form [23,24] and air humidity increases. Litter surfaces can be rewetted during humid nights, representing one type of diel dry-and-rewet cycle.

(iii) Litter may play an important role in soil carbon flux of tropical forests. A litterfall manipulation experiment in Costa Rican rainforest stressed the considerable role of litterfall in soil carbon cycling [25]. Litterfall, both as a direct source of CO2 and as an input of soil organic matter, should be expected to play an important role in soil heterotrophic respiration, especially in the rapid-turnover tropical rainforest [26,27].

4.2. Temperature Sensitivity of the Studied Tropical Forests

We have little information on temperature sensitivity of tropical forests except that collected from incubation studies [28,29]. The equatorial tropical forests have a narrow temperature range. Observations across seasons found a clear dependence of respiration upon water rather than temperature [8,9]. The studied tropical forest has an annual temperature range of up to 10 °C, providing the possibility to investigate temperature sensitivity.

Many models have been used to describe the temperature dependence of soil respiration [30,31]. We compared four commonly used models to derive the temperature sensitivity index (Q_{10}) of soil heterotrophic respiration (Table 1). The Q_{10} value derived from the Q_{10} model was 2.54. Nevertheless, we found that the Kirschbaum–O'Connell model worked best in describing the temperature dependence from a statistical perspective. The Kirschbaum–O'Connell model stressed a steep decline in Q_{10} with temperature (Figure 7). The reason why models implying a decrease in Q_{10} with temperature work better than those with fixed Q_{10} is still unknown. This might be related to substrate availability as suggested in modeling work [32].

The Q_{10} of R_h estimated using the Q_{10} model (2.54) was higher than that collected from incubation studies, i.e., a forest in northern Southeast Asia (2.2) [28] and in Australia (1.43–2.21) [29]. The Q_{10} value was also higher than that of the total soil respiration of a nearby non-dipterocarp forest (2.03–2.36) [33]. Soil water content was maintained at a near-saturation level across the seasons owing to the exclusion of transpiration water losses (Figure 2). The confounding effect of soil water content on Q_{10} estimation was minimized. The Q_{10} value here should, thus, be representative of the studied forest. This might be related to the latitude and mean annual temperature of this site. The site is close to the Tropic of Cancer with a mean annual temperature of around 22 °C. Given that Q_{10} decreases with mean annual temperature, the Q_{10} of the studied forest was expected to be higher than that of forests closer to the equator [34].

4.3. Variation of Soil Respiration among Microhabitats and Implications for Carbon Balance

Topographic fragmentation is strong in the studied site [13], and spatial heterogeneity is an important dimension that needs to be taken into account under such circumstances [15]. Soil respiration of the three habitats varied strongly (Figure 5). The highest value was nearly three times that of the lowest. The arithmetical mean R_h of the three microhabitats was 4.00 $\mu mol \cdot m^{-2} \cdot s^{-1}$, which can be easily extrapolated to 1516 $gC \cdot m^{-2} \cdot year^{-1}$. As reported before, the net primary production of this forest is 1198 $gC \cdot m^{-2} \cdot year^{-1}$ [13]. Thus, the studied forest was proposed as a net carbon source. However, this is not a convincing estimation. In fact, the forest gap only accounts for a small part of the total forest land [35]. A weighted averaging could produce a more sound estimation of soil respiration for the whole stand. We adopted a 20 × 20 m resolution habitat classification map to accomplish the weight averaging [35]. Gap, low valley, and others accounted for 6.2%, 28.0%, and 65.8% land area of the 20 ha plot, respectively. The weight-averaged soil heterotrophic respiration was 3.33 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (equal to 1262 $gC \cdot m^{-2} \cdot year^{-1}$). This indicates a near-carbon-neutral state or a very slight carbon source for the studied forests. However, this remains a rough estimation because the microhabitats discussed here should be examined at a scale of several meters, as this is more reliable and convincing than the arithmetical averaging method.

Uncertainties arising from measuring techniques were slight in this study because of the following:

    (i)   The use of the commercial Li-8100/8150 avoided the problem caused by fan mixing. Some self-design chambers use the convenience of fans for mixing [6]. This violates the basic principle of soil efflux measurement with the static chamber method [17]. Research has shown that soil CO2 efflux increases linearly with wind speed [16].

    (ii)   Sufficient trench depth: Trenching is still a major method used to separate soil heterotrophic and autotrophic respiration. Given insufficient trench depth, heterotrophic respiration cannot be completely separated [36]. We trenched to a depth of 1.2–1.3 m; at this depth, no visible root could be found, and rock was semi-weathered.

    (iii)   Reliability of the method used to calculate fluxes: Linear regression should be used appropriately in calculating CO2 efflux with a static chamber [37], as inappropriate application of this method could lead to serious bias. The present study avoided this bias (cf. Li-8100/8150 manual).

5. Conclusions

We investigated patterns, components, and controls of a mixed dipterocarp forest in China. Several conclusions could be drawn.

    (i)   Soil respiration varied strongly among the microhabitats and played a crucial role in stand-level ecosystem carbon balance assessment. A weight-averaged estimate taking this spatial variation into account could give more defensible soil respiration and net carbon budget assessment than arithmetical averaging.

    (ii)   The unexpected diel pattern on heterotrophic respiration was probably related to moisture dynamics.

    (iii)   The Kirschbaum–O'Connell model was the best model describing the temperature dependence of soil heterotrophic respiration among the four models. The temperature sensitivity index (Q_{10}) varied among models. The value derived using the Q_{10} model was 2.54.

Author Contributions: Methodology and investigation, Z.-H.T., J.-F.Z. and Z.-Y.L.; writing—original draft preparation, J.-F.Z.; writing—review and editing, Z.-H.T. and Z.-Y.L.; data curation, J.-F.Z. and L.-Y.Y.; supervision, J.-K.S. All authors read and agreed to the published version of the manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

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