



# Article Seasonal Dynamics of Soil Respiration and Its Autotrophic and Heterotrophic Components in Subtropical Camphor Forests

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Abstract: On a global scale, soil respiration ( $R_s$ ), representing the CO<sub>2</sub> flux between the soil surface and the atmosphere, ranks as the second-largest terrestrial carbon (C) flux. Understanding the dynamics between  $R_s$  and its autotrophic ( $R_a$ ) and heterotrophic ( $R_b$ ) components is necessary for accurately evaluating and predicting global C balance and net ecosystem production under environmental change. In this study, we conducted a two-year root exclusion experiment in subtropical China's Camphor (Cinnamomum camphora (L.) Presl.) forests to assess seasonal changes in Ra and Rh and their relative contributions to Rs. Additionally, we examined the influence of environmental factors on the dynamics of Ra, Rh, and Rs. Our results showed that seasonal mean Rs values were 2.88  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>, with mean R<sub>a</sub> and R<sub>h</sub> of 1.21 and 1.67  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>, respectively, in the studied forests. On an annual basis, the annual values of mean R<sub>s</sub> in the studied forests were  $405 \pm 219$  g C m<sup>-2</sup> year<sup>-1</sup>, with R<sub>h</sub> and R<sub>a</sub> accounting for  $240 \pm 120$  and  $164 \pm 102$  g C m<sup>-2</sup> year<sup>-1</sup>, respectively. The seasonal mean ratio of  $R_h$  to  $R_s$  ( $R_h/R_s$ ) was 58%, varying from 45 to 81%. Seasonal changes in Rs and Rh were strongly correlated with soil temperature but not soil water content. Both  $R_{\rm h}$  and  $R_{\rm s}$  increased exponentially with the average soil temperature measured in the topsoil layer (about 5 cm), with  $Q_{10}$  values of 2.02 and 1.73 for  $R_h$  and  $R_s$ , respectively. Our results suggest that the composition and activity of soil microbes and fauna play a primary role in releasing carbon flux from soil to the atmosphere in the studied forest ecosystems.

Keywords: camphor forest; root respiration; microbial respiration; carbon cycling; soil CO<sub>2</sub> efflux

# 1. Introduction

Soil CO<sub>2</sub> efflux (FCO<sub>2</sub>), often referred to as soil respiration (R<sub>s</sub>), is the second-largest carbon (C) flux between terrestrial ecosystems and the atmosphere. On a global scale, land plants absorb approximately 120 Pg ( $10^{15}$  g) of C per year through the photosynthetic process. Concurrently, the R<sub>s</sub> process releases around 68–98 Pg of C back into the atmosphere annually [1–3]. Therefore, R<sub>s</sub> is a critical component of the global C cycle, significantly affecting global climate [4,5]. In terrestrial ecosystems, R<sub>s</sub> is the result of soil autotrophic respiration (R<sub>a</sub>, mainly from roots and associated rhizosphere respiration) and soil heterotrophic respiration (R<sub>h</sub>, from microbes and soil fauna respiration) [6,7]. R<sub>a</sub> is primarily influenced by root growth and productivity, photosynthesis capacity, C substrate



Citation: He, P.; Yan, W.; Peng, Y.; Lei, J.; Zheng, W.; Zhang, Y.; Qi, Y.; Chen, X. Seasonal Dynamics of Soil Respiration and Its Autotrophic and Heterotrophic Components in Subtropical Camphor Forests. *Forests* **2023**, *14*, 2397. https://doi.org/ 10.3390/f14122397

Academic Editor: Brian D. Strahm

Received: 3 November 2023 Revised: 25 November 2023 Accepted: 5 December 2023 Published: 8 December 2023



**Copyright:** © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). availability, soil organic matter, and nutrient contents [4,7,8]. Since different C sources, biological processes, and metabolic pathways are involved in  $R_s$  components, the feedback of the  $R_a$  and  $R_h$  components to environmental changes varies. Hence, partitioning  $R_s$  into  $R_a$ and  $R_h$  components is important. It can provide insight into the C cycle and sequestration in terrestrial ecosystems under natural and anthropogenic disturbances [4,8].

Numerous studies have focused on partitioning  $R_s$ , yet significant uncertainty and variability persist in estimates within forest ecosystems [9,10]. For example, we summarized and evaluated the advantages and disadvantages of three commonly used methods for partitioning  $R_s$  into  $R_a$  and  $R_h$  components in plant communities [11]. The ratio of  $R_h$  to  $R_s$  varied from 10 to 90% in terrestrial ecosystems, depending on vegetation types and seasonal variations [12]. On average, R<sub>a</sub> contributed 45.8% in forest ecosystems and 60.4% in non-forest ecosystems to  $R_s$  [13]. Based on soil FCO<sub>2</sub> data from 54 forest sites, we summarized that  $R_a$  and  $R_h$  were approximately evenly partitioned, ranging between 50 and 60% [4]. Recent studies found that in longleaf pine forests,  $R_h$  dominated  $R_s$ , with an annual ratio of  $R_h$  to  $R_s$  ranging from 66 to 96% [14,15]. In addition, the  $R_a$ ,  $R_h$ , and Rs processes are largely regulated by environmental factors, primarily soil temperature  $(T_{soil})$  and soil water content ( $W_{soil}$ ) [16].  $R_s$  exhibits a distinct seasonal pattern, primarily controlled by T<sub>soil</sub> [17], and the annual pattern of precipitation indirectly influences the interannual variation of  $R_s$  by affecting  $W_{soil}$  in subtropical forests [18]. Thus, significant variations in the proportions of Ra and Rh components to Rs highlight the need for further research to better understand the mechanisms that regulate R<sub>a</sub>, R<sub>h</sub>, and R<sub>s</sub> dynamics in forest ecosystems.

Among the methods used to partition  $R_a$  and  $R_h$ , studies have used trenching method as a root exclusion method to separate  $R_a$  and  $R_h$  from  $R_s$  [19,20]. Previous studies showed that the trenching technique is easy to use in field conditions, adaptable to various circumstances, yields reasonable values, and produces comparable partitioning results with other methods [9,20]. Nevertheless, the trenching method used to separate the contribution of  $R_a$  and  $R_h$  components to total  $R_s$  has limitations [21]. The literature extensively discusses major shortcomings associated with this method, including (1) the potential influence of newly deceased fine and coarse roots [22]; (2) disturbance effects caused by the act of trenching [23]; (3) alterations in soil water regimes resulting from the artifacts of the trenching treatment [24]. Significantly, recent research has highlighted that trenching artifacts may lead to increased soil water content due to reduced water uptake and elevate the relative proportion of  $R_h$  to  $R_s$  due to inputs from newly severed dead roots [25].

Subtropical evergreen broad-leaved forests in Southern China are globally significant biomes that play a crucial role in C cycling and sequestration at regional, national, and global scales [26,27]. The total net ecosystem productivity (NEP) in East Asian subtropical forests has been  $0.72 \pm 0.08$  Pg C year<sup>-1</sup>, accounting for 8% of the global forest NEP [28]. Camphor (Cinnamomum camphora (L.) Presl.) forests are a significant part of evergreen broad-leaved forests in this region. This species contains volatile chemical compounds in all plant parts, which have allelopathic effects on certain plant species and natural habitats [29]. In Camphor forests, numerous studies have examined the characteristics of the Rs process, but little is known about how it contributes to Ra and Rh components in these forest ecosystems. The purpose of the current study was to examine the contribution patterns of R<sub>a</sub> and R<sub>h</sub> components of R<sub>s</sub> in a Camphor forest ecosystem. We hypothesized that (a) R<sub>h</sub> would contribute more to R<sub>s</sub> than R<sub>a</sub> based on the findings from our previous experiments and other studies in subtropical forests; (b) the relative proportions of  $R_h$ and  $R_a$  to  $R_s$  would change following seasonal variations in the study region's weather conditions. The specific objectives of this project were: (1) to quantify the seasonal and annual fluxes of  $R_s$ ,  $R_a$ , and  $R_h$ ; (2) to explore the respective contributions of  $R_a$  and  $R_h$ components to  $R_s$ ; (3) to examine the relationships between  $T_{soil}$  and  $W_{soil}$  and  $R_s$  and its components.

#### 2. Materials and Methods

# 2.1. Study Site

The experimental site is located in Tianjiling National Park in Changsha, Hunan province, China, at coordinates 113°02′–01′ E and 28°06′–07′ N. This region features a low mountain and hill terrain, with elevations ranging from 46 to 114 m above sea level and slopes varying from 5° to 20°. The site experiences a typical monsoon subtropical climate, characterized by a mean annual temperature of 17.2 °C, with the lowest monthly mean air temperature in January at 4.7 °C and the highest in July at 29.4 °C. The mean annual rainfall is 1422 mm, falling primarily between April and August. Annual relative humidity averages above 80%.

The dominant tree species in the experimental area included Camphor (*Cinnamomum camphora* (L.) Presl.), Chinese sweet gum (*Liquidambar acalycina*), Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook.), Masson pine (*Pinus massoniana* Lamb.), and slash pine (*Pinus elliottii*). The soil beneath these forests has been classified as a typical clay-loam red soil developed from slate parent rock, corresponding to Alliti-Udic Ferrosols as per the World Reference Base for Soil Resources (CRG-CST 2001). The soil has an acidic pH, with an average of 5.0 in the surface layer (0–10 cm) and a soil organic C content of  $19.77 \pm 0.68 \text{ mg g}^{-1}$  at a depth of 10 cm.

For this study, the selected Camphor forests were established as pure forests in 1990, commencing with an initial tree density of 1600 trees per hectare. The mean diameter at breast height (DBH) was 14.9 cm, and the mean tree height was 12.6 m. These Camphor forests were in a young stage of growth and development. The understory plant species at the study site consisted of *Sassafeas tsumu* Hemsl.; *Clerodendron cyrtophyllum Turcz; Cinnamomum camphora; Symplocos caudata* Wall. ex A. DC.; *Lophantherum gracile Brengn.; Nephrolepis auriculata* Trimen; *Miscanthus floridulus* Warb; and *Phytolacca acinosa* Roxb.

### 2.2. Experiment Design

Soil FCO<sub>2</sub> measurements in the 20-year-old Camphor forests began in August 2010 and were routinely conducted for two years. The experiment was conducted following a completely random design (CRD). Three  $20 \times 20$  m sites were established within the study area's Camphor forests. Each site was divided into six square plots, each with a side length of 2 m (area 4 m<sup>2</sup>). Among these plots, three plots were randomly selected for trenched treatments, and the remaining three were designated as un-trenched treatments. This arrangement resulted in three pairs of trenched and un-trenched plots within each forest site.

The sites and plots were chosen based on their relatively homogeneous topography within the Camphor forests. To minimize the potential influence of tree proximity on soil FCO<sub>2</sub> rate measurements, the selected plots were positioned near the center of the tree lines within the forests. These plots represented factors within the experiment, with trenched plots devoid of living roots and un-trenched plots serving as the control, representing intact areas with living roots. The trenched plot was a cubic block with a narrow ditch, approximately 0.2 m wide, excavated to a depth of 0.8 m along the four sides of the square. This depth extended below the rooting zone, where minimal root presence was observed [29]. The excavated trenches excluded live tree roots. To create a barrier, we placed several 2 mm thick polyethylene plastic sheets around the trenches, extending them to the trench's depth. Afterward, we backfilled the trenches with excavated soil, carefully removing herbaceous vegetation from the trenched plots by hand throughout the study to minimize soil disturbance.

Each trenched plot was equipped with a PVC respiration collar measuring 10.5 cm in diameter and 4.5 cm in height, inserted at approximately 2 cm into the soil. These collars were installed at least one week before the first measurement of  $R_s$  and remained in place throughout the experiment. To mitigate both root decay and soil disturbance effects resulting from trenching and the use of flux chambers, the trenched plots were established two months before the experiment, and the PVC collars were inserted into the

soil at least one week before the initial  $R_s$  measurement, where they remained for the entire study duration. The un-trenched plot was located 35 m away from the trenched plot and remained undisturbed, with no excavation or removal of herbaceous vegetation. In each un-trenched plot, a PVC respiration collar was installed for soil FCO<sub>2</sub> measurements.

#### 2.3. Field Measurements

Soil FCO<sub>2</sub> rates were measured in the field biweekly from August 2010 to August 2012 using a portable infrared gas analyzer (LI-COR 8100, LI-COR Inc., Lincoln, NE, USA) equipped with a chamber. During measurements, the respiration collar was sealed with a soil chamber connected to the infrared gas analyzer. All measurements were conducted between 10:00 a.m. and 2:00 p.m. to avoid diurnal fluctuations. For data analysis, we used the mean value of the two measurements per plot.

Soil FCO<sub>2</sub> rates were expressed as  $\mu$ mol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>. Measurements from trenched plots represented R<sub>h</sub> due to root exclusion, while measurements from un-trenched plots reflected the total R<sub>s</sub>, including both R<sub>a</sub> and R<sub>h</sub>. As a result, R<sub>a</sub> can be estimated by subtracting R<sub>h</sub> from R<sub>s</sub> [29,30].

During each soil FCO<sub>2</sub> measurement,  $T_{soil}$  was monitored using a soil thermocouple probe (LI-COR 8100-09 TC, LI-COR Inc., Lincoln, NE, USA) inserted into the soil at a depth of 5 cm below the surface. We also measured  $W_{soil}$  (volumetric soil water content, %) in the topsoil layer (0–5 cm) using an ECH2O EC-5 soil moisture sensor (METER Environment, formerly Decagon Devices, Inc., Pullman, WA, USA) [8]. Both  $T_{soil}$  and  $W_{soil}$  measurements were obtained outside the PVC collars.

# 2.4. Data Analysis

We assessed the differences in soil FCO<sub>2</sub> between trenched and un-trenched plots using analysis of variance (ANOVA). To meet the normality and homoscedasticity assumptions of ANOVA, the original R<sub>s</sub> and R<sub>h</sub> data were log-transformed. A repeated two-way ANOVA was applied to assess the effects of treatments and monitoring time on soil FCO<sub>2</sub> rates, T<sub>soil</sub>, and W<sub>soil</sub>. The ratios R<sub>a</sub>/R<sub>s</sub> and R<sub>h</sub>/R<sub>s</sub> were used to represent the respective contributions of the R<sub>a</sub> and R<sub>h</sub> components. All statistical analyses were performed with a significance level set at *p* < 0.05 using SAS statistical software (Version 8, SAS Institute Inc., Cary, NC, USA, 1999–2001). Nonlinear regression analysis was employed to model the relationship between R<sub>s</sub> and T<sub>soil</sub> and W<sub>soil</sub>. To assess the temperature sensitivity of R<sub>s</sub>, we calculated the Q<sub>10</sub> index, defined as the difference in respiration rates over a 10 °C interval, using the following equation:

Q

$$_{10} = e^{10b}$$
 (1)

where, b is the constant fitted into Equation (1).

#### 3. Results

During the two-year study period, soil respiration ( $R_s$ ) rates were significantly lower in the trenched plots than in the control plots of the Camphor forests (p < 0.05).  $R_s$  rates ranged from 0.61 to 3.55 µmol m<sup>-2</sup> s<sup>-1</sup> in trenched plots and from 0.73 to 5.85 µmol m<sup>-2</sup> s<sup>-1</sup> in un-trenched plots (Figure 1). On average, soil FCO<sub>2</sub> rates were reduced by approximately 60% in trenched plots ( $1.67 \pm 0.13 \mu$ mol m<sup>-2</sup> s<sup>-1</sup>, Mean  $\pm$  SD) compared to un-trenched plots ( $2.88 \pm 0.09 \mu$ mol m<sup>-2</sup> s<sup>-1</sup>) (Table 1).

Throughout the two-year study, there was significant seasonal variability in soil FCO<sub>2</sub> rates. The mean monthly contributions of each  $R_s$  component varied, with  $R_a/R_s$  contributing between 25.5 and 51.4% to  $R_s$  (Table 2).



**Figure 1.** Seasonal changes in soil temperature at 5 cm soil depth, topsoil soil water content at the 5 cm layer, and soil respiration rate in trenched and un-trenched plots in the Camphor forest during the study period. Error bar indicates standard error  $\pm$  s.e.

Time (Year)	Treatment	Soil FCO <sub>2</sub> Rate ( $\mu$ mol m <sup>-2</sup> s <sup>-1</sup> )	T <sub>soil</sub> (°C)	W <sub>soil</sub> (%)
2010–2011	Trenched Un-trenched	$1.77 \pm 0.12$ a $3.09 \pm 0.09$ b	$16.86 \pm 0.07$ a $16.88 \pm 0.09$ a	$32.26 \pm 2.12$ a $28.41 \pm 1.86$ b
2011–2012	Trenched Un-trenched	$1.56 \pm 0.15$ a $2.67 \pm 0.10$ b	$16.11 \pm 0.06$ a $16.09 \pm 0.19$ a	$27.45 \pm 1.75$ a $24.45 \pm 1.95$ b
Average	Trenched Un-trenched	$1.67 \pm 0.13$ a $2.88 \pm 0.09$ b	$16.49 \pm 0.06$ a $16.49 \pm 0.14$ a	$29.85 \pm 1.94$ a $26.43 \pm 1.90$ b

**Table 1.** Annual mean soil CO<sub>2</sub> efflux (FCO<sub>2</sub>) rates, soil temperature ( $T_{soil}$ ), and soil water content ( $W_{soil}$ ) from trenched and un-trenched plots in Camphor forests during the study period.

Note: Values are presented as mean  $\pm$  standard deviation. Distinct letters within the same column and year indicate significant differences (p < 0.05).

**Table 2.** Average monthly patterns of  $R_a$ ,  $R_h$ , and  $R_s$  (µmol m<sup>-2</sup> s<sup>-1</sup>), and a relative proportion of  $R_a$  component to  $R_s$  (%) in studied forests over the 2-year study period.

Month	R <sub>a</sub>	R <sub>h</sub>	R <sub>s</sub>	R <sub>a</sub> /R <sub>s</sub>
January	0.354	0.718	1.071	33.0
February	0.287	0.771	1.058	27.1
March	0.300	0.959	1.259	23.8
April	1.453	1.785	3.237	44.9
May	1.537	2.337	3.874	39.7
June	2.568	2.704	5.272	48.7
July	1.783	2.477	4.260	41.9
August	1.950	2.577	4.527	43.1
September	1.650	1.558	3.207	51.4
October	1.445	1.574	3.019	47.9
November	0.832	1.324	2.155	38.6
December	0.413	1.207	1.620	25.5

Note: Ra, autotrophic respiration; Rh, heterotrophic respiration; Rs, total soil respiration.

The monthly relative proportion of  $R_a$  to  $R_s$  was consistently below 50% for all months throughout the year, except in September (Table 2). In addition, the ratio of  $R_a/R_s$  reached its maximum in summer and autumn, and its minimum in winter. On average, the ratio of  $R_a/R_s$  was lower than that of  $R_h/R_s$  for all four seasons, with a difference of about 10% in summer and autumn, 40% in winter, and 30% in spring at the study site (Table 2). While  $T_{soil}$  exhibited significant variation throughout the study, there were no notable differences in  $T_{soil}$  between trenched and un-trenched plots (p > 0.05). However, trenching had statistically significant effects on  $W_{soil}$  (p < 0.005). In general, the soil was generally dry during the autumn and winter seasons and wetter in the spring and summer.

The maximum and minimum  $T_{soil}$  values were 26.1 and 26.3 °C in July 2011, and 3.9 and 3.9 °C in January 2011 for trenched and un-trenched plots, respectively (Figure 1). The mean values of  $W_{soil}$  were consistently higher in trenched plots than in un-trenched plots, with an average value of 29.9 and 26.4% in trenched and un-trenched plots, respectively (Figure 1). The peak value of  $W_{soil}$  occurred in June 2010 at 37.9 and 33.6%, whereas the minimum value was recorded in September 2011 at 15.1 and 13.9% for trenched and untrenched plots (Figure 1). Soil FCO<sub>2</sub> rate was significantly correlated with  $T_{soil}$  (p < 0.0001) (Figure 2), but not with  $W_{soil}$  (p > 0.05) (Figure 3). Instantaneous soil FCO<sub>2</sub> rates were exponentially related to  $T_{soil}$ , and the corresponding  $Q_{10}$  was 1.73 for trenched plots and 2.02 for un-trenched plots.



**Figure 2.** The relationships between soil respiration rates and soil temperature  $(T_{soil})$  in un-trenched plots (**A**) and trenched plots (**B**) in the Camphor forest over the study period.



**Figure 3.** The relationships between soil respiration rates and soil water content ( $W_{soil}$ ) in un-trenched plots (**A**) and trenched plots (**B**) in the Camphor forest over the study period.

### 4. Discussion

Trenched plots in Camphor forests exhibited a substantial reduction in soil respiration rates ( $R_s$ ) over two years compared to un-trenched control plots. On average,  $R_s$  rates in trenched plots decreased by approximately 42% compared to control plots. Similar observations of  $R_s$  reduction due to root exclusion were reported in other studies. For instance, a nearby Chinese fir forest showed a 28% decrease in  $R_s$  in trenched plots than in un-trenched plots. One study observed a 39% reduction in  $R_s$  rates one year after trenching in a lowland tropical forest [31]. In a 30-year-old beech stand, there was a decrease of around 36% in the annual soil carbon efflux observed in the trenched plots compared

to control plots. Additionally, in subtropical evergreen broad-leaved forests, trenching reduced soil FCO<sub>2</sub> by approximately 17% over a three-year period [32]. This reduction in annual soil FCO<sub>2</sub> in trenched plots was primarily associated with root exclusion, as  $R_a$  is a significant component of total soil respiration in forest ecosystems [29]. These findings highlight the consistent impact of root exclusion on reducing soil respiration rates in various forest types, emphasizing the importance of considering root contributions in assessing soil C dynamics [33]. The results from the current study indicate a relative contribution of 42% for  $R_a$  to  $R_s$  in evergreen broad-leaved Camphor forests, which aligns well with the ranges previously reported for subtropical forests (Table 3).

Forest Type	R <sub>a</sub> /R <sub>s</sub> Mean (Range)	References
Camphor forest	41.9 (19.0-55.0)	This study
Chinese fir forest (5 years old)	27.1	[34]
Chinese fir forest (22 years old)	32.6 (13.3-55.7)	[29]
Chinese fir forest	40.3	[35]
Natural evergreen forest	47.8	[35]
Broadleaf and needle leaf mixed forest	26.75	[36]
Bamboo forest	10.98	[36]
Monsoon evergreen broad-leaf forest (about 400 years old)	22.1-35.4	[37]
Pine forest (about 60 years old)	18.1-26.1	[37]
Pine and broad-leaf mixed forest (~60 years old)	20.0-29.1	[37]
Evergreen broad-leaved forest (20–120 years old)	21.4-32.3	[34]
Moist forest	33	[32]

Table 3. Comparison of R<sub>a</sub> component contribution (%) to R<sub>s</sub> in different subtropical forest types.

Note: R<sub>a</sub>: autotrophic respiration, R<sub>s</sub>: total soil respiration.

Further research indicates that both  $R_a$  and  $R_h$  are influenced by temperature and precipitation. Studies analyzing global patterns found that an increase in mean annual temperature led to higher  $R_a$  and  $R_h$  rates, with increases of 12.9 and 16.1 g C m<sup>-2</sup> year<sup>-1</sup>, respectively, for every 1 °C rise [38].  $R_a$  was found to increase by 44.5 g C m<sup>-2</sup> year<sup>-1</sup> for every 100 mm increase in mean annual precipitation (MAP) when MAP was <1000 mm, while  $R_h$  increased linearly by 15.0 g C m<sup>-2</sup> year<sup>-1</sup> for every 100 mm increase in MAP [38]. The study suggested that the fractional contribution of  $R_a$  to  $R_s$  may be greater in boreal forests than in temperate forests, reflecting regional differences in ecosystem dynamics [39]. These study findings contribute to our understanding of the variation in  $R_a$  and  $R_h$  contributions to  $R_s$ , highlighting a multitude of factors influencing these dynamics with the potential to exhibit regional distinctions [40].

Bond–Lamberty et al. [1] established a relationship between Ra and Rs, expressed as RC =  $-0.66 + 0.16 \times \ln (R_s)$ , indicating that  $R_a$  contribution may vary depending on  $R_s$ . By employing this model, we estimated the root contribution (RC) of our study site. The calculated RC value averaged 30.1%, ranging from 17.6 to 37.0% across the Camphor forests under investigation. These estimated values were slightly lower than our field measurements, where the RC averaged 41.9% with a range of 25.5–51.4% (Table 2). It is worth noting that this variation may be attributed to limitations in the data sources used to develop the model. The data sources were primarily derived from 54 forest sites, with a significant focus on boreal and temperate forests, a minimal representation of tropical forests, and none from subtropical regions [41]. As a result, the RC–RS relationship, while potentially reliable globally, may show significant deviations at a local scale [42]. This finding may be due to a myriad of biotic and abiotic factors, including  $T_{soil}$ ,  $W_{soil}$ , soil nutrients, soil microbial composition, tree species, and forest types, which can have specific influences on  $R_a$  at local or site-specific scales [21]. Therefore,  $R_a$ - $R_s$  relationships developed at a regional level may not provide precise estimates of the respective contributions of  $R_a$  and  $R_h$  components within a specific site [4,38,39].  $R_a$  appeared to be predominantly governed by physiological activities associated with root growth [9], below-ground C

allocation [39], and phenological characteristics of tree species [37]. On the other hand, R<sub>h</sub> appeared to be primarily regulated by substrate availability and biophysical conditions within the soil [43]. This seasonal pattern aligns with findings that reported a similar trend in R<sub>a</sub> dynamics, reaching its highest value in late July due to maximal fine-root biomass and living fungal biomass during the summer and autumn [44]. During the growing season, R<sub>a</sub> comprises both maintenance respiration and growth respiration, whereas, in the dormant season, R<sub>a</sub> primarily consists of maintenance respiration [45]. Additionally, the positive relationship between maintenance respiration and temperature can lead to higher maintenance respiration during summer (the growing season) when temperatures are elevated, in contrast to winter (the dormant season) when temperatures are lower [46].

Previous studies have demonstrated that both  $T_{soil}$  and  $W_{soil}$  are crucial factors controlling  $R_a$ ,  $R_h$ , and  $R_s$  [47,48]. Soil CO<sub>2</sub> effluxes closely followed seasonal and diurnal variations in  $T_{soil}$ , as indicated by our findings (Figure 1).  $T_{soil}$  accounted for over 80% of the seasonal variation in soil FCO<sub>2</sub> in the Camphor forest, showcasing a strong correlation between soil FCO<sub>2</sub> and  $T_{soil}$ . This observation aligns with the results of previous studies [29]. However, it is worth noting that most  $R_s$ - $T_{soil}$  relationships may not accurately reflect the actual temperature response of  $R_s$ . Therefore, these temperature response functions are likely inadequate for predicting the effects of climate change on  $R_s$  [49]. In addition, climate change is expected to affect water availability by comprehensively altering the amount, distribution, and frequency of precipitation and evaporation [50]. To gain a better understanding of  $R_s$  in changing environments, considering both biotic and abiotic interactions is essential [49].

In our experiment, we observed that  $W_{soil}$  consistently remained higher in trenched plots compared to control plots (Figure 1). This finding is likely attributable to trenching, which increased  $W_{soil}$  by reducing evapotranspiration [30] and root transpiration [29]. Notably, we observed that the correlations between soil  $FCO_2$  and  $W_{soil}$  were not statistically significant (p > 0.05), which is consistent with previous research on Chinese fir forests [29], an old-growth coniferous forest [51], and boreal forests [30]. In reality, the soil  $FCO_2-W_{Soil}$ relationship is complex, and the influence of W<sub>soil</sub> on soil FCO<sub>2</sub> rates is often modulated by the  $T_{soil}$ -soil FCO<sub>2</sub> relationship under a threshold value of  $W_{soil}$  [48]. When the threshold value of W<sub>soil</sub> is reached, it creates conditions in the soil that promote the diffusion of both oxygen and soluble substrates, thereby enhancing soil FCO<sub>2</sub> rates [52]. However, if W<sub>soil</sub> falls significantly below or rises above this threshold value, it can impede biological processes and alter the relationship between W<sub>Soil</sub> and soil FCO<sub>2</sub>. For instance, it was reported that when soil exceeded 0.11 m<sup>3</sup> m<sup>-3</sup>, soil FCO<sub>2</sub> rates were positively correlated with T<sub>soil</sub> in a temperate Douglas fir forest, but when W<sub>soil</sub> was below this threshold, the soil FCO<sub>2</sub>-T<sub>soil</sub> relationship became largely decoupled [53]. Additionally, one of the authors of this study conducted research in a wet-dry savanna in Northern Australia and observed similar trends in the  $T_{soil}$ -soil FCO<sub>2</sub> relationship and the threshold value of  $W_{soil}$  [54]. In this wet–dry savanna, the threshold value of  $W_{soil}$  was about 0.07 m<sup>3</sup> m<sup>-3</sup>, with soil FCO<sub>2</sub> rates showing a significant positive correlation with T<sub>soil</sub> when W<sub>soil</sub> was above this threshold and a weak relationship when  $W_{soil}$  was below 0.07 m<sup>3</sup> m<sup>-3</sup> [43]. This weak relationship between soil FCO<sub>2</sub> and T<sub>soil</sub> under lower W<sub>soil</sub> conditions can be attributed to limitations in the soluble substrate [52,54]. Furthermore, the status of  $W_{soil}$  directly affects the composition and activity of the soil microbial community, which can significantly influence the  $T_{soil}$ -soil FCO<sub>2</sub> relationship [55]. Different microbial communities have distinct optimal W<sub>soil</sub> conditions for their survival, growth, and development. Changes in W<sub>soil</sub> conditions can create different habitats for soil microbial communities, which directly impacts R<sub>h</sub> and R<sub>s</sub> [56]. A meta-analysis indicates that the response of organism respiration to water stress varies widely across functional types, such as soil fauna, bacteria, and fungi [57].

Although we did not observe a tight relationship between soil FCO<sub>2</sub> and  $W_{soil}$  in the present study, it is plausible that  $W_{soil}$  indirectly affects soil FCO<sub>2</sub> rates through  $Q_{10}$  regulation [53]. We found that the temperature sensitivity of  $R_s$  was reduced in trenched

plots ( $Q_{10} = 1.73$ ) compared to un-trenched plots ( $Q_{10} = 2.02$ ) in the current study. This observation suggests that the temperature sensitivity of  $R_h$  was less pronounced than that of  $R_s$ . Such findings indirectly support the conclusion that  $Q_{10}$  values derived from field measurements, including  $R_a$ , could potentially overestimate the response of  $R_h$  to temperature changes on a future, warmer Earth [38].

## 5. Conclusions

In summary, this study has shown that  $R_h$  plays a significant role, contributing approximately 60% to the annual  $R_s$  in Camphor forests. Our estimates of the relative contributions of  $R_s$  components align with those reported in subtropical forests.  $T_{soil}$  is the primary factor controlling the seasonal variability of  $R_s$ ,  $R_h$ , and the  $R_h/R_s$  ratio. The proportion of  $R_a$  to  $R_s$  reaches its peak during the growing season and is at its lowest when the trees are dormant. Considering the significant concentration of the  $R_h$  component in the soil respiration ( $R_s$ ) of the studied forests, the formulation of suitable management practices focusing on the biophysical environment and microbial community of soil in subtropical forests becomes imperative. Such practices can significantly help reduce  $CO_2$  emissions from soils, mitigating rising  $CO_2$  concentrations in the atmosphere.

**Author Contributions:** Conceptualization, P.H., W.Y. and X.C.; methodology, P.H., W.Y., Y.P. and X.C.; validation, J.L., W.Z., Y.Z. and Y.Q.; formal analysis, Y.P., J.L., W.Z., Y.Z. and Y.Q.; investigation, P.H., J.L. and W.Z.; resources, J.L., Y.Z. and Y.Q.; writing—original draft preparation, P.H. and Y.P; writing—review and editing, Y.P., J.L. and X.C.; supervision, W.Y. and X.C.; project administration, P.H. and W.Y.; funding acquisition, W.Y. and X.C. All authors have read and agreed to the published version of the manuscript.

**Funding:** The study was supported by the National Key Research and Development Program of China (2020YFA0608101), the Joint Funds of the National Natural Science Foundation of China (U21A20187), and a 'Shu Ren Scholar' plan of Central South University of Forestry and Technology. We would like to thank Cao Zhang, Wancai Wang, and Dongjun Zou for their field and laboratory measurements.

**Data Availability Statement:** The data presented in this study are available on request from the corresponding author.

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

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