Autotrophic and heterotrophic contributions to soil respiration in a subtropical camphor tree forest

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Abstract

Understanding the contributions of autotrophic respiration (R_a) and heterotrophic respiration (R_h) to total soil respiration (R_s) is necessary for accurate prediction of global carbon balance and net ecosystem production under environmental change. In this research, annual R_s and R_h and estimated were investigated by using a root trenching experiment in a Camphor tree (*Cinnamomum camphora*) forest in subtropical China for two years to qualify the relative contribution of R_a and R_h components to R_s, and to determine the environmental factors that control the seasonal changes in R_a, R_h and R_s. The results showed that annual mean R_s was 405 ± 219 gC m^{-2} $year^{-1}$ in the studied forests, of which R_h and R_a were 240 ± 120 gC m^{-2} $year^{-1}$ and 164 ±102 gC m^{-2} $year^{-1}$, respectively. The contribution of R_h to R_s averaged 58.1%, ranging from 45 to 81%. The seasonal changes in R_s and R_h were highly correlated with soil temperature, but not to soil water content. Our results suggest microbial community and activity make a primary contribution to carbon flux released from soil to atmosphere in the studied forest ecosystems.

KEYWORDS

camphor tree forest, root respiration, microbial respiration, carbon cycling, soil CO_2 efflux, soil temperature, soil moisture.

1 INTRIDUCTION

Soil CO_2 efflux (FCO_2) (often called soil respiration, R_s) is recognized as the second largest carbon (C) flux between terrestrial ecosystems and the atmosphere. It is one of the key components of global C cycle, which has significant effects on global climate (Raich et al., 2002; Schlesinger & Andrews, 2000). In terrestrial ecosystems, R_s is the result of soil autotrophic respiration (R_a, mainly from roots and associated rhizosphere respiration) and soil heterotrophic respiration (R_h, from microbes and soil fauna respiration) (Davidson et al., 2006; Schulze, 2002; Tang & Baldocci, 2005). R_a is mostly dependent on root growth and productivity, photosynthesis capacity and photosynthate allocation patterns, while R_h is largely influenced by the belowground C substrate availability, soil organic matter and nutrient contents (Bond-Lamberty et al., 2004; Tang & Baldocci, 2005). Because different C sources, biological processes and metabolic pathways are involved in R_s components, the feedbacks of the R_a and Rh components to environmental changes vary. Hence, partitioning R_s into R_a and R_h components is important. It can provide further understanding of the C cycle and sequestration in terrestrial ecosystems under natural and anthropological disturbances (Bond-Lamberty et al., 2004; Tang & Baldocci, 2005).

Many studies have been conducted in partitioning Rs, but there still exists great uncertainty and variability among estimates within forest ecosystems (Lee et al., 2003; Yan et al., 2019). For example, Hanson et al. (2000) reviewed and summarized the advantages and disadvantages of three common-used methods: component integration, root exclusion, and isotopic approaches for partitioning R_s into R_a and R_h components in plant communities. By reviewing published estimates of soil FCO_2 rates from 51 forest and cropland studies, they found that the ratio of R_h to R_s ranged from 10 to 90% in terrestrial ecosystems, depending on vegetation types and seasons of the year. The contribution of R_a to R_s averaged 45.8% and 60.4% for forest and non-forest ecosystems, respectively. Bond-Lamberty et al. (2004) summarized soil FCO_2 data from 54 forest sites and found that R_a and R_h were roughly evenly partitioned between 50% and 60%. They pointed out that there might be a relationship between R_a and R_h at the global scale, because the dynamics of these two soil FCO_2 components ultimately depend on forest C balance and photosynthate supply. Recently, studies found R_s was dominated by R_h in longleaf pine forests, with annual ratio of R_h to R_s from 66 to 96% (ArchMiller & Samuelson, 2016; Collins et al., 2005). The large variations of proportion of R_a and R_h components to R_s implied studies should be conducted for further understanding of the mechanisms that regulate the dynamic properties of R_a, R_h and R_s in forest ecosystems.

Among the several methods used to partition R_a and R_h, the trenching method has been widely used in the studies to separate R_a and R_h from R_s (Hogberg et al., 2009; Tian et al., 2011; Zeng et al., 2016). Previous studies have found this technique was easy to operate under field conditions and was suitable for maintaining in various circumstances. Additionally, this approach provided reasonable values and had a comparable partitioning effect with other methods (Lee et al., 2003; Zeng et al., 2016). Nevertheless, the trenching method to separate the contribution of Ra and Rh components to total Rs has its weaknesses (Kuzyakov & Larionova, 2005; Savage et al., 2018). The major shortcomings have been recognized and discussed in the literature, including (1) influence of newly deceased fine and coarse roots (Kuzyakov, 2010), (2) disturbance effect due to digging the trenches (Kuzyakov & Larionova, 2005), and (3) alteration of soil water regime resulted from the artefacts of the trenching treatment (Comstedt et al., 2011). Recently, Savage et al., (2018) revealed that the artifacts of the trenching might raise soil water content because of the reduced water uptake, and increase relative proportion of R_h to R_s due to new severed dead roots inputs.

The subtropical evergreen broad-leaved forests in southern China are recognized as one of the most important biomes on earth and they play an important role in C cycling and sequestration at regional, national and global scales (Yan et al., 2013; 2014). The Camphor tree (*Cinnamomum camphora*) forests represent an important type of the evergreen board-leaved forests in this region. This species contains volatile chemical compounds in all plant parts, which provides a negative effect of allelopathy to some plant species and natural habitats (Tian, 2005). A few studies have been carried out to investigate the characteristics of R_s process in Camphor tree forests, but little is known about relative contributions of R_a and R_h components to R_s in the forest ecosystems. The purpose of the current study was to examine the contribution patterns of R_a and R_h components of R_s in a Camphor tree forest ecosystem. We hypothesized that the relative proportion of R_h and R_a to R_s would be different in the studied forest due to different response of these two components to environmental factors. The specific objectives of this project were: (1) to quantify seasonal and annual fluxes of R_s, R_a and R_h, (2) to explore the respective contribution of R_a and R_h to R_s, and (3) to examine the relationships between soil temperature (T_{soil}) and soil water content (W_{soil}) and R_s.

2 MATERIALS AND METHODS

2.1 Study sites

The experimental site was situated in the Tianjiling National Park in Changsha, Hunan province, China (28° 6′ 7″ N, 113° 1′ 20″ E). The area was characterized by a low mountain and hill region varying from 46 to 114 m above sea level. Topography varied from 5 to 20^0 slopes. The site had a typical monsoon subtropical climate, with a mean annual temperature of 17.2 ºC and the lowest monthly mean air temperatures in January (4.7 ºC) and highest in July (29.4 ºC). The mean annual rainfall was 1422 mm, most of which occurred from April to August. Mean annual relative humidity was > 80%. The experimental area was dominated by camphor tree (*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 was classified as a typical clay-loam red soil earth developed from slate parent rock, which was equal to Alliti-Udic Ferrosols according to the World Reference Base for Soil Resources (CRG-CST 2001). Soil was acidic with an average pH of 5.0 on the surface (0-10 cm). Soil organic carbon content at 10 cm surface layer was 19.77±0.68 mg g^{-1}. In the present study, the selected Camphor tree forests were planted as pure forests in 1995 with an initial tree density of 1600 trees/ha. The mean DBH was 14.9 cm and mean tree height was 12.6 m. The Camphor tree forests were in a young stag of growth and development. The understory plant species in the study site were consisted of *Sassafeas tsumu* Hemsl.; *Cinnamomum camphora*; *Symplocos caudata Wall. ex* A. DC.; *Clerodendron cyrtophyllum* Turcz; *Nephrolepis auriculata* Trimen; *Lophantherum. gracile* Brengn.; *Miscanthus floridulus* Warb.; and *Phytolacca. acinosa* Roxb.

2.2 Experiment design

The experiment was treated as a completely random design. Three 20 m × 20 m sites were established in the Camphor tree forests in the study area. The experimental design consisted of six square plots with the side length of 2 m (area 4 m^2). Three plots were selected randomly for trenched treatments, and three remaining plots were un-trenched treatments. Three pairs of trenched and un-trenched plots were set up in each forest site. The criterion for selecting sites and plots was relatively homogeneous in topography of the Camphor tree forests. In order to eliminate the effects of distance from trees on the measurements of soil FCO_2 rate, the selected plots were roughly located in the middle of the tree lines of the forests., in which the trenched (without living roots) and un-trenched treatments (control, intact area with living roots) were the factors.

The trenched plot was a cubic block, where a narrow ditch (about 0.2 m) was dug down to a depth of 0.8 m along the four sides of the square, which was below the rooting zone which few roots exist in the forests (Tian, 2005). Live tree roots were excluded from the dug trenches. Several polyethylene plastics sheets (1 mm thick each) were placed around and to the depth of the trench. Then the ditches were backfilled with the excavated soil. The herbaceous vegetation was carefully removed from the trenched plots by hand throughout the study with minimal soil disturbance. One PVC respiration collar (10.5 cm in diameter and 4.5 cm in height) was installed in each of trenched plots. The PVC collar was inserted approximately 2 cm in the soil. Once installed, the collar was left in place throughout the course of the experiment. In order to minimize both root decay and soil disturbance effects from the trenching and utilization of the flux chamber, the trenched plots were developed two months and the PVC collars were inserted into the soil at least one week prior to the first measurement of R_s. The PVC collars were kept in place through the entire study.

The un-trenched plot was located 35 m apart from the trenched plot. The un-trenched plot was kept intact without digging and herbaceous vegetation removal. A PVC respiration collar per plot was set up for soil FCO_2 measurements.

2.3 Field measurements

Soil FCO_2 rates were measured every two weeks from August of 2010 to August of 2012 in the field with a portable infra-red gas analyzer (LI-COR 8100, LI-COR Inc., Lincoln NE, USA) equipped with a chamber. When measuring, the respiration collar was closed with a soil chamber connected to the infra-red gas analyzer. All measurements were always made between 10:00 AM to 2:00 PM to avoid diurnal fluctuations. The average value of the two measurements per plot was used for data analysis. The soil FCO2 rate was expressed as µmol CO2 m-2 s-1. Soil FCO2 measurements from trenched plots presented Rh from soil because of roots exclusion, while soil FCO2 measurements from un-trenched plots presented the total Rs including both Ra and Rh. Consequently, Ra can be estimated by subtracting Rh from Rs (Peng & Thomas, 2006; Tian et al., 2011).

On each soil FCO2 measurement occasion, T_{soil} was monitored with a soil thermocouple probe (LI-COR 8100-09 TC, LI-COR Inc, Lincoln, Nebraska, USA), inserted into soil to a depth of 5 cm below the soil surface. W_{soil} (volumetric soil water content, %) in the topsoil layer (0-5 cm) was measured using an ECH2O EC-5 soil moisture sensor (Decagon, USA). Both T_{soil} and W_{soil} were measured at the vicinal outside of PVC collars.

2.4 Data analysis

The differences in the soil FCO_2 from trenched and un-trenched plots were evaluated through an analysis of variance (ANOVA). In order to satisfy the normality and homoscedasticity assumptions of ANOVA, the original R_s and R_h data were log-transformed. A repeated two-way ANOVA was used to evaluate the influences of treatments and monitoring time on soil FCO_2 rates, T_{soil}, and W_{soil}. R_a/R_s and R_h/R_s were defined as the respective contribution of R_a and R_h components, respectively. All statistical analyses were conducted at $p < 0.05$ with a SAS statistical package (Version 8, SAS Institute Inc, CaryNC, 1999-2001).

Nonlinear regression analysis was used to describe the response of R_s to T_{soil} and

W_{soil}.

To determine the temperature sensitivity of R_s, the index of Q_{10}, defined as the difference in respiration rates over a 10 ºC interval was estimated using an equation:

$$Q_{10} = e^{10b} \quad (1)$$

where, b is the constant fitted into equation 1.

3 RESULTS

R_s rates were significantly lower in trenched plots than in control plots in the Camphor tree forests over two years studied period ($p < 0.05$). R_s rates ranged 0.61-3.55 µmol m^{-2} s^{-1} and 0.73-5.85 µmol m^{-2} s^{-1} in trenched and un-trenched plots, respectively (Figure 1). On average, soil FCO_2 rates were reduced by about 60% in trenched plots (1.67 ± 0.13 µmol m^{-2} s^{-1}, Mean ± SD) compared to the un-trenched plots (2.88 ± 0.09 µmol m^{-2} s^{-1}) (Table 1).

TABLE 1 HERE

TABLE 2 HERE

Over the 2-year study, seasonal variability of soil FCO_2 rate was very high. The mean monthly contribution of each component to R_s varied, with R_a/R_s contributing from 25.5% to 51.4% to R_s (Table 2). Based on the biweekly measurements, the cumulative annual mean R_s, R_h and R_a were 405 ± 219, 240 ± 120 and 164 ±102 gC m^{-2} $year^{-1}$, respectively.

The relative proportion of R_h to R_s was minimum in summer and autumn, and maximum in winter. On average, the ratio of R_h/R_s was higher than that of R_a/R_s for the four seasons and the difference between R_h/R_s and R_a/R_s was about 10% in summer and autumn, 40% in winter and 30% in spring in the study site (Figure 2).

FIGURE 1 HERE

FIGURE 2 HERE

Although T_{soil} exhibited high variation during the studied period, there were no significant differences of T_{soil} between trenched and un-trenched plots ($P > 0.05$). However, trenching had statistically significant effects on W_{soil} ($p < 0.005$). Soils generally were drier in the autumn and winter and wetter in the spring and summer. The maximum and minimum T_{soil} were 26.1°C and 26.3°C in July 2011, and 3.9°C and 3.9°C in January 2011 in 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 average value at 29.9% and 26.4% in trenched and un-trenched plots, respectively (Figure 1). The peak value of W_{soil} occurred in June of 2010 with 37.9% and 33.6% and the minimum value of W_{soil} occurred in September 0f 2011 with 15.1% and 13.9% in trenched and un-trenched plots (Figure 1).

Soil FCO_2 rate was strongly correlated with T_{soil} ($P < 0.0001$) (Figure 2), but not with W_{soil} ($P > 0.05$). Instantaneous soil FCO_2 rates were exponentially related to T_{soil} and the soil FCO_2-T_{soil} relationships can be described using the following models in trenched and un-trenched plots:

Trenched plots: Soil FCO_2 rate $=0.6108e^{0.0549T}$ $R^2 = 0.8187$ (2)

Un-trenched plots: Soil FCO_2 rate $=0.7852e^{0.0701T}$ $R^2 = 0.8836$ (3)

T_{soil} explained 88% and 82% of the variation in R_s and R_h, respectively. The corresponding Q_{10} was 1.73 for trenched plots and 2.02 for un-trenched plots.

4 DISCUSSION

When compared to un-trenched plots, R_s rates in trenched plots were significantly reduced on two years basis. On average, R_s rates decreased about 60% in trenched plots compare to the control. A similar finding was observed in nearby Chinese fir forests, in which R_s was decreased about 28% in trenched plots compared with that in un-trenched plots (Tian et al., 2011). The phenomenon of R_s reduction in trenched plots in the Camphor tree forests has occurred in many previous studies. For instance, Sayer and Tanner (2010) reported that trenching had reduced R_s rates by 39% one year later after the trench treatment in a lowland tropical forest. Annual soil carbon efflux was 0.42 Kg C m^{-2} $year^{-1}$ on the trenched plots in a 30-year-old beech stand, which was about 36% lower than in the control plots (Epron et al., 1999). Compared to the subtropical evergreen broad-leaved forests, Schaefer et al. (2009) found that trench plots reduced about 17% soil FCO_2 rate than control plots over all three-year period. The reduction of annual soil FCO_2 rate in trenched plots is obviously attributed to root excision because R_a was an important R_s component.

TABLE 3 HERE

Our results of annual mean relative contribution of R_a (42%) and R_h (58%) to R_s in this evergreen board-leaved Camphor tree forest were well with the ranges of previously reported values for subtropical forests (Table 3). The relative proportion of R_a and R_h components to R_s varied widely, depending on many factors such as different forest types, forest ages, experiment methods, root dimensions, land use changes, and environmental conditions (Hanson et al., 2000). Specifically, it was reported R_a accounted for 52-83% of R_s in six temperate forests (Wang & Yang, 2007) and 27-71% in a cool-temperate deciduous forest (Lee et al., 2003). Hanson et al. (2000) pooled about 50 republished results and found that the relative contribution of the R_a to R_s ranged from 10 to 90%, with mean values of 45-50% for forest ecosystems. Based on published data from 54 forest sites, Bond-Lamberty et al. (2004) reported that R_a was closely related annual R_s and the root contribution (RC) could be expressed as: $RC = -0.66 + 0.16 \times \ln(R_s)$. Wang et al. (2010) analyzed the global patterns of R_a and R_h to temperature and precipitation and found that R_a and R_h would increase 12.9 and 16.1 g C m^{-2} yr^{-1}, respectively, for every 1 ^{0}C increase in mean annual temperature. R_a would increase 44.5 g C m^{-2} yr^{-1} for every 100 mm increase in mean annual precipitation (MAP) when MAP < 1000 mm and would be kept a relatively constant when MAP > 1000 mm, while R_h increased lineally by 15.0 g C m^{-2} yr^{-1} for every 100 mm increase in MAP. Hogberg et al. (2009) suggested that the fractional contribution of R_a to R_s may be greater in boreal than in temperate forests.

Using the model: $RC = -0.66 + 0.16 \times \ln(R_s)$ (Bond-Lamberty et al., 2004), we estimate the RC value for our study site. The estimate of RC averaged 30.1%, ranged from 17.6% to 37.0% in the studied Camphor tree forests. These estimated data were slightly lower when compared to our field measurements: averaged 41.9% with the range of 25.5-51.4% (Table 2). We thought that the low RC values estimated by the model were likely related to the limitation of the data sources for developing the model. The data sources covered 54 forest sites, but most of the data came from the boreal and temperate forests. Only three data were derived from tropical forest sites, and none from subtropical regions. The RC-R_S relationship might be reliable at the global scale but would have relatively large deviation at a local scale bias. Many biotic and abiotic factors, such as T_{soil}, W_{soil}, soil nutrients, soil microbial composition, tree species, and forest types had specific effects on R_a at a local/site scale (Hanson et al., 2000; Lee et al., 2003; Wang & Yang, 2007; Wang et al., 2010). Thus, the R_a-R_s relationship developed from a regional level may not provide accurate estimates of respective contribution of R_a and R_h components in a specific site (Bond-Lamberty et al., 2004; Wang et al., 2010).

Our studies indicated that the relative proportion of R_a and R_h components to R_s varied with season, reflecting the different mechanisms adopted by R_a and R_h to response the environmental changes (Hanson et al., 2000). R_a was mainly controlled by physiological activities associated to root growth (Lee et al., 2003), below-ground carbon allocation (Hogberg et al., 2009), phenological characters of tree species (Yi et al., 2007), while R_h was mostly regulated by substrate availability and biophysical environments in soil systems (Cisneros-Dozal et al., 2006). The higher relative proportion of R_a component during the summer and autumn, and lower in winter coincided with largest biomass production occurring in growing season, and lowest root activity when the roots were dormant in the winter (Tian 2005). Pumpanen et al. (2015) revealed a similar seasonal patterns of R_a dynamics in which the contribution of R_a reached its highest value in late July, which attributes to the maximal fine-root biomass production and living fungal biomass in summer and autumn. Tang and Baldocchi (2005) concluded the seasonal changes in R_a/R_s reflected the seasonal activity of roots. R_a came only from maintenance respiration when root was in a dormant state, but it was comprised of both maintenance respiration and growth respiration during the growing season. In addition, because of the positive relations between maintain respiration and temperature, the maintenance respiration could be higher in the summer (growing season) with higher temperature than in the winter (dormant season) (Ryan et al., 1996).

Previous studies have demonstrated both T_{Soil} and W_{soil} were the most important factors controlling R_a, R_h and R_s (Gutiérrez del Arroyo & Wood, 2021; Ma et al., 2019). The soil FCO_2 also closely followed the seasonal and diurnal variations in T_{soil}. In this study, we found the similar patterns that the seasonal changes in R_s and R_h closely followed the dynamics of T_{soil} (Figure 1). T_{soil} could explain over 80% of the seasonal variation in soil FCO_2 in Camphor tree forests. The strong correlation between soil FCO_2 rate and T_{soil} was consistent with results from other studies reported previously (Tian et al., 2011). However, most of the R_s-T_{soil} relations could not be reflected in the actual temperature response of R_s and thus these temperature response functions would likely fail to predict effects of climate change on R_s (Subke & Bahn, 2010). To better understanding of R_s in changing environments, the biotic and abiotic interactions should be considered (Subke & Bahn, 2010). In our experiment, W_{soil} was constantly higher in trenched plots than control plots (Figure 1). This was highly likely that trenching increased W_{soil} by reducing evapotranspiration (Peng & Thomas, 2006) and roots transpiration (Tian et al., 2011). The correlations between soil FCO_2 rate and W_{soil} were not significant ($p > 0.05$). In our experiment, W_{soil} was constantly higher in trenched plots than control plots (Figure 1). This was highly likely that trenching increased W_{soil} by reducing evapotranspiration (Peng &

Thomas 2006) and roots transpiration (Tian *et al*. 2011). The correlations between soil FCO_2 rate and W_{soil} were not significant (p > 0.05). Our results were in line with findings of several previous researches, such as in Chinese fir forests (Tian et al., 2011), an old growth coniferous forest (Sulzman et al., 2005) and boreal forests (Peng & Thomas 2006). In fact, the soil FCO_2-W_{Soil} relationship was complex and the influence of W_{soil} on soil FCO_2 rate was often modified by the T_{soil}-soil FCO_2 relationship under a threshold value of W_{soil} (Ma et al., 2019). When the threshold value of W_{soil} was reached, the physical, chemical and biological conditions in the soil might facilitate the diffusion of both oxygen and soluble substrates, and thus enhance soil FCO_2 rate (Linn & Doran, 1984). If W_{soil} was far below or above its threshold value, biological processes could be impeded and the W_{Soil}-soil FCO_2 relationship would be changed. For example, Jassal et al. (2008) reported that when W_{soil} was > 0.11 m^3 m^{-3}, soil FCO_2 rate was positively correlated to T_{soil} in a temperate Douglas fir forest, but when W_{soil} was below this threshold value, the soil FCO_2-T_{soil} relationship was largely decoupled. One author of this project conducted a study at a wet-dry savanna of northern Australia and found the similar results dealing with T_{soil}-soil FCO_2 and threshold value of Wsoil (Chen et al., 2002). The threshold value of W_{soil} was 0.07 m^3 m^{-3} in the studied wet-dry savanna. The soil FCO_2 rate exhibited a significantly and positively to T_{soil} when W_{soil} was > 0.07 m^3 m^{-3}. However, the relations between soil FCO_2 and T_{soil} was weak when W_{soil} was < 0.07 m^3 m^{-3}. The weak relationship between soil FCO_2 and T_{soil} under lower W_{soil} was likely attributed to soluble substrate limitation (Chen et al., 2002; Linn & Doran, 1984). Additionally, W_{soil} status directly affected the composition and activity of soil microbial community, which might significantly alter T_{soil}-soil FCO_2 relationship (Gray et al., 2011). Different microbial communities had various optimum W_{soil} for their survival, growth and development. Changes in W_{soil} conditions might result in a different habitat for soil microbial communities (Schnürer et al., 1986), which directly affected R_h and R_s.

In addition, although no obviously tight relationship was found between soil FCO_2 and W_{soil} in the present study, W_{soil} may indirectly affect soil FCO_2 rate through regulating Q_{10} (Jassal et al., 2008). 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, implying temperature sensitivity of R_h was less than that of R_s. This funding might indirectly support the conclusion that Q_{10} values derived from field measurements, including R_a, could overestimate the response of R_h to temperature changes on a future warmer earth (Wang et al., 2010).

In this study, the magnitude of the effects of trenching method on the estimate of the contribution of Ra and Rh to total Rs was unknown but would tend to increase Rs from the trenched plots. Thus, one should take these effects into account when interpreting the data in this experiment. A suitable methodology was recently proposed to overcome the disadvantage resulted from the trenching method (Savage et al., 2018). They pointed out utilizes a Bayesian modeling framework could quantifying and correcting the artifacts of new-fresh dead roots and altered soil moisture (Savage et al., 2018).

In conclusion, the study found R_h provided a major contribution (about 60%) to annual R_s in the Camphor tree forests. Our estimate of relative contribution of R_s components was comparable to that reported in subtropical forests. T_{soil} was the most important factor controlling the seasonal variation of R_s, R_h and R_h/R_s. The proportion of R_a to R_s reached the peak when the forests were in a growing season, but the lowest when the trees were dormant. Given high relative concentration of R_h component in R_s in the studied forests, to develop suitable management practices on soil biophysical environment and microbial community in subtropical forests plays a critical role in decreasing emission of CO_2 from soils and thus mitigating the rising of CO_2

concentration in the atmosphere.

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CONFLICTS OF INTERESTS

None declared.

AUTHORS CONTRIBUTION

W.Y. and X.C. designed the research project. W.Y. and W.Z conducted field measurements. Y.P. provided data analysis. All authors provided input on interpretation of the results and contributed to writing the original draft. Y.P. and X.C provided review and editing of the manuscript.

DATA AVA I L A B I LIT Y S TATEMENT

Data are available from Dryad data repository.

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TABLE 1 Annual mean soil CO_2 efflux (FCO_2) rates, soil temperature (T_{soil}) and soil water content (W_{soil}) from trenched and un-trenched plots in Camphor tree forests during the study period

Time	Treatment	Soil FCO_2 rate (μmol.m^2.s^{-1})	T_{soil} (°C)	W_{soil} (%)
2010-11	Trenched	1.77±0.12a	16.86±0.07a	32.26±2.12a
	Un-trenched	3.09±0.09b	16.88±0.09a	28.41±1.86b
2011-12	Trenched	1.56±0.15a	16.11±0.06a	27.45±1.75a
	Un-trenched	2.67±0.10b	16.09±0.19a	24.45±1.95b
Average	Trenched	1.67±0.13a	16.49±0.06a	29.85±1.94a
	Un-trenched	2.88±0.09b	16.49±0.14a	26.43±1.90b

Note: Values are mean ± standard deviation. Different letters on the same column and same year indicate significant differences ($p < 0.05$).

TABLE 2 Average monthly patterns of R_a, R_h and R_s (µmol.m^2.s^{-1}), and relative proportion of R_a component to R_s (%) over 2 years study period

Month	R_a	R_h	R_s	R_a/R_s
Jan.	0.354	0.718	1.071	33.0
Feb.	0.287	0.771	1.058	27.1
Mar.	0.300	0.959	1.259	23.8
Apr.	1.453	1.785	3.237	44.9
May	1.537	2.337	3.874	39.7
Jun.	2.568	2.704	5.272	48.7
Jul.	1.783	2.477	4.260	41.9
Aug.	1.950	2.577	4.527	43.1
Sep.	1.650	1.558	3.207	51.4
Oct.	1.445	1.574	3.019	47.9
Nov.	0.832	1.324	2.155	38.6
Dec.	0.413	1.207	1.620	25.5

Note: R_a: autotrophic respiration, R_h: heterotrophic respiration, R_s: total soil respiration.

TABLE 3 Comparison of contribution (%) of R_a component to R_s **in different subtropical forest types**

Forest type	R_a/R_s Mean (Rang)	References
Camphor tree forest	41.9 (19.0-55.0)	This study
Chinese fir forest (5 years old)	27.1	(Wang et al., 2017)
Chinese fir forest (22 years old)	32.6 (13.3-55.7)	(Tian et al., 2011)
Chinese fir forest	40.3	(Yang et al., 2007)
Natural evergreen forest	47.8	(Yang et al., 2007)
Broadleaf and needle leaf mixed forest	26.75	(Yu et al., 2015)
Bamboo forest	10.98	(Yu et al. ,2015)
Monsoon evergreen broad-leaf forest (about 400 years old)	22.1-35.4	(Yi et al., 2007)
Pine forest (about 60 years old)	18.1-26.1	(Yi et al., 2007)
Pine and broad-leaf mixed forest (~ 60 years old)	20.0-29.1	(Yi et al., 2007)
Evergreen broad-leaved forest (20-120 years old)	21.4-32.3	(Wang et al., 2017)
Moist forest	33	(Schaefer et al., 2009)

Note: R_a: autotrophic respiration, R_s: total soil respiration.

Figure legends

Figure 1. Seasonal changes in soil temperature at 5 cm soil depth, soil water content of the 5 cm topsoil layer and soil respiration rate in trenched and un-trenched plots in the Camphor tree forest over the study period. Error bar indicates standard error: ±s.e.

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