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ORIGINAL PAPER

Comparative Analysis of Soil Respiration Dynamics and Heterotrophic Respiration Sensitivity to Warming in a Subalpine Coniferous Forest and a Subtropical Evergreen Broadleaf Forest in Southwest China

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Abstract

To quantify variations in the components of soil respiration (*Rs*), elucidate the impact of warming on heterotrophic respiration (*Rh*) in subalpine coniferous forest (LJ) and in subtropical evergreen broadleaf forest (ALS), and discern differences in the dominant regulating factors of soil respiration components between the two forest ecosystems. This study used multi-channel automated soil efflux chambers with three treatments: control (CK), trenching (NR), and trenching with warming (NRW) in LJ and ALS in Southwest China. The results reveal that *Rs* was higher in ALS than in LJ, and the ratio of *Rh* to *Rs* was significantly higher in LJ than in ALS. Although soil temperature (*ST*) and soil moisture (*SM*) also identified the main controlling factors of *Rs*, *Rh*, *Ra*, and the warming effect of *Rh* when considering carbon cycle modeling, the sensitivity of *Rs* to temperature (Q_{10}) was not significantly different between *Rs*, *Rh*, and *Ra* for both forests. The greater warming effect on *Rh* in LJ than in ALS is due to the combination of lower temperatures, recalcitrant organic matter, and slower litter decomposition in subalpine coniferous forests. This study confirmed that *Rs*, *Rh* and *Ra* had positive correlation with *ST* and *SM* for two ecosystems. This study has proven that the greater the warming effect of *Rh* is, the greater the contribution of *Rh* to *Rs* becomes, and the lesser the contribution of *Ra* to *Rs* in LJ becomes compared to that of ALS.

Keywords Soil respiration · Heterotrophic respiration · Fractions · Temperature sensitivity · Warming effect

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1 Introduction

Soil is the largest organic carbon pool (Lal 2004),and soil respiration (*Rs*) is the second largest flux of carbon dioxide (CO_2) in terrestrial ecosystems (Raich and Schlesinger 1992). The study of *Rs* is crucial due to its substantial impact on global carbon (C)cycling and its integral role in biogeochemical models (Wang et al., 2006). Therefore, *Rs* ranges from approximately 68–80 Pg C yr^{-1} on a global scale (Raich and Schlesinger 1992), accounting for approximately 50–75% of the total respiration of terrestrial ecosystems (Hanson et al., 2000). *Rs*, comprising both heterotrophic respiration (*Rh*) and autotrophic respiration (*Ra*), is the combined result of *Rh*, driven by CO_2 emissions from soil microorganisms and fauna during the decomposition of soil organic matter (SOM) and their own metabolic processes, and *Ra*, primarily originating from plant roots (Hanson et al., 2000; Kuzyakov 2006)as outlined by (Kuzyakov 2006). To better understand the contributions of *Ra* and *Rh* to C cycling in forest ecosystems, previous studies have developed root trenches (or girdling) to quantify soil respiration components (Hashimoto et al. 2015; Hinko-Najera et al. 2015; Wang et al. 2019; Zhou et al. 2021a). The results indicate that the contribution of *Rh* to *Rs* ranges from 45 to 70%, declining with increasing annual *Rs* (Subke et al. 2006). Thus, the ratio of *Ra* to *Rs* will increase with annual *Rs*. The ratio of *Ra/Rh* is responsive to variations in both environmental and substrate conditions, and in certain circumstances, it may be elevated. However, regional differences in environmental conditions can affect the magnitude of this effect (Lei et al. 2022). Generally, *Rh* and *Ra* are associated with SOM decomposition by soil microbes and fauna seeing that components of *Rs* is released from a result of decomposition of SOM and plant litter by soil microbes and through plant roots and soil fauna (Dias de Oliveira et al. 2020). Thus, the contributions of *Ra* and *Rh* to *Rs* sufficiently reflect the responses of *Rs* to changing temperatures (Rankin et al. 2022). The direction of these contributions can underestimate the feedback of global climate change in forest ecosystems and to C cycling via accurate measurements and assessments of *Rs* contributions (Rankin et al. 2022).As the biogeochemical processes of *Rs* are highly temperature sensitive (Duan et al. 2019), the responses of *Rs* to warming also influence future trajectories of climate change (Romero-Olivares et al. 2017). In recent decades, soil warming experiments have been developed in many forest ecosystems to clarify and investigate the warming effect on *Rs* and its temperature sensitivity (Aguilos et al. 2013) and show that *Rh* and *Ra* sensitivity to temperature varies across research sites. For example, *Rh* increased with increasing temperature in Norway spruce (Schindlbacher et al. 2008), and a negative response to soil warming was observed in a model (Zhou *et al. 2010)*. Some studies have shown that warming increased *Rh* but decreased *Ra* in grasslands (Li et al. 2013; Verburg et al. 2009). The warming effect brings about different responses of *Ra* and *Rh* in forest ecosystems, and understanding these responses of *Ra* and *Rh* from forest soils to warming is important for predicting the global C cycle at different latitudes (Liu et al. 2019). In contrast to *Ra*, it is imperative to scrutinize the reactions of *Rh* to climate change. This is crucial, as the forthcoming impacts of C-climate feedback are contingent upon the climate sensitivity of net terrestrial C fluxes, with particular emphasis on *Rh* (Konings et al. 2018).Furthermore, *Rs* is predominantly influenced by several key factors, encompassing soil temperature (*ST*), soil moisture (*SM*), substrate availability, soil texture, structure, density, nutrient content, and pH levels. (Włodarczyk et al. 2008). It is noteworthy that among abiotic factors, *ST* and *SM* stand out as the principal determinants governing the dynamics of *Rs* (Davidson and Janssens 2006). Many studies have shown the response of *Rs* to temperature increase and the relationship between *Rs* and *ST* by using Q_{10} (Shi et al. 2019), which is presented by an exponential function. Q_{10} usually expresses the change per 10 °C of temperature increase in *Rs* (Liang et al. 2017). The temperature sensitivity of Rs is generally represented by Q_{10} decreasing from polar to temperate to tropical regions (Meyer et al. 2018). Furthermore, Q_{10} values for both *Rhand R*a are individually linked to pertinent influencing factors, including substrate quantity and quality, microbial organisms and enzyme kinetics, photosynthetic activity, and fine root biomass(Han and Jin 2018). The variation in Q_{10} responses to climate change among forest sites arises due to differences in forest floor type, soil physical and biochemical characteristics, as well as variations in temperature and precipitation patterns (Luan et al. 2013). Detecting these variations in Q_{10} across forests under conditions of global warming is crucial in predicting the impacts of climate change on forestcarbon dynamics (Yang et al., 2022).

Moreover, changing temperatures could affect C cycling in terrestrial ecosystems, including not only subalpine coniferous forests but also subtropical evergreen broadleaf forests, which may alter future climate change together with positive or negative feedback (Liu et al. 2018). The effect of warming on *Rs* have been investigated in various ecosystems, including grasslands (Roland et al. 2015), boreal coniferous forests dominated by Norway spruce (Bronson et al. 2008), temperate forests (Schindlbacher et al. 2015), and subtropical evergreen forests (Wu et al. 2016). In these studies, different warming experiments were conducted to stimulate the potential effects of climate change on terrestrial ecosystems (Mitchell et al. 2022). The effect of warming on *Rs* has been found to vary among ecosystems and caused the contributions of *ST* and *SM* to *Rs* to vary during warming periods. However, the specific effect of warming treatment of approximately 2 °C on *Rs* and the main factors driving this effect are not well understood in forest ecosystems. Subtropical evergreen broadleaf forests and subalpine coniferous forests are the main C sinks in the Northern Hemisphere. Furthermore, soil C is the most important factor for C budgets (Lei et al. 2019). Additionally, *Rs* responses to warming among subalpine coniferous forests and subtropical evergreen broadleaf forests are urgently needed to estimate global C cycle.

To evaluate the impact of warming on *Rs* and the sensitivity of *ST* and *SM* in diverse ecosystems, we implemented a soil warming experiment employing a multichannel automated chamber system in both a subalpine coniferous forest in Lijiang (LJ) and a subtropical evergreen broadleaf forest in Ailaoshan or Ailao Mountain (ALS), situated in Yunnan Province, Southwest China. The primary aims of this study were to quantify variations in the components of *Rs*, elucidate the impact of warming on *Rh* in these forest ecosystems, and discern differences in the dominant regulating factors of *Rs, Rh* and *Ra* between the two forest ecosystems. Our hypothesis posited that subtropical evergreen broadleaf forests would exhibit a lower warming effect on *Rh*, whereas this effect would be subject to debate in subalpine coniferous forests. The study's findings affirmed that *Rs*, *Rh*, and *Ra* were consistently higher in ALS compared to LJ throughout the study period. These results contribute to a more comprehensive understanding of C cycling in these distinct forest ecosystems.

2 Materials and Methods

2.1 Study Sites

In this study, we examined two sites (LJ and ALS) in Yunnan, Southwest China. Among them, LJ is a subalpine coniferous forest situated in the experimental area of the Lijiang Provincial Nature Reserve, which includes Lijiang Forest Ecosystem Positioning Research Station. This area is located in the foothill of Yulong Snow Mountain where the climate in this region experiences a summer monsoon wet season, lasting from May to October, and the Qinghai-Tibetan Plateau circulation and westerly winds occurred in the dry season, which lasts from November to April(Luo et al. 2016). Wet season starts at first week of May (1 May, 2015 to 7 May, 2015) and ends at last week of October (24 October, 2015 to 30 October,2015) for LJ and ALS. And dry season of starts at first week of November (24 November, 2015 to 31 November, 2015) and ends at last week of April (24 April, 2015 to 30 April, 2015) for LJ and ALS. Wet season and dry season of LJ and ALS are same because LJ and ALS are located in Yunnan, Southwest China. In rainy or wet season, the average soil moisture content level ranges from 20 to 45%, and the dry season shows levels of 15–35% in LJ. Annual evaporation levels reach 966.1 mm, and relative humidity reaches 82%. Local forests are mainly classified as cold-temperate coniferous forests, and the main dominant tree species in LJ are *Picea likiangensis* (Pinaceae), *Abies forrestii* (Pinaceae), *Quercus guayavifolia* (Fagaceae), *Acer pectinatum* (Sapindaceae), and *Padus brachypoda (Rosaceae)* (Huang et al. 2017). The first three species mentioned namely, *Lijiang spruce, Sichuan-Yunan fir*, and *Quercus glabra* (Fagaceae), are the dominant and constructive species in the forest layer of this study (Fei et al. 2018).

The second research site, ALS, is located in Jingdong County, Yunnan Province and in the northern part of the Ailaoshan Natural Reserve. This area belongs to monsoon climate condition. In this area, an old-growth subtropical evergreen broadleaf forest is widely distributed and well protected. Subtropical montane evergreen broad-leaved forest (dominated by three subtropical oak species, *Lithocarpushancei* (Fagaceae), *Lithocarpus xylocarpus* (Fagaceae) and *Castanopsiswattii* (Fagaceae) persists in the Ailaoshan Natural Reserve (Schaefer et al. 2009). The strata of the Ailao Mountain forest include canopy (18–25 m), shrub (1–3 m), and herb layers (< 0.5 m) (Tan et al. 2011). From a conservation point of view, the forest is well managed (Tan et al. 2013). The soil volumetric water content exceeds 35% in the upper 50 cm (Gong et al. 2011). The overview of two forest ecosystems including latitude and longitude, elevation, soil type, basal area, leaf area index, tree density, tree height, and stand age, etc… are described in Table 1.

2.2 Soil Warming Experiments

The rate of continuous *Rs* was measured in the two different forest ecosystems (LJ and ALS) using a multichannel automated chamber system designed by Liang et al. 2003. The system was composed of 12 automatic chambers (90 × 90 × 50 cm) and a control box for LJ, and 20 automatic chambers (90 × 90 × 50 cm) and a control box for ALS. For LJ, the 12 chambers were divided into three treatments (four chambers per treatment): control (CK), trenching (NR), and infrared light warming together with trenching (NRW), where litter removal treatment (NL) was not applied. In ALS, the 20 chambers were divided into four treatments (five chambers per treatment). The multichannel automated chamber system was established to measure soil CO_2 effluxes with three treatments in December 2014 for LJ and with four treatments in October 2010 for ALS. One-year data from these three treatments of soil warming experiment in 2015 for LJ and ALS was used in this study. The temperature increase rate for warming plot was 2.4

Table 1 Comparison between subalpine coniferous forest of Lijiang (LJ) and subtropical evergreen broadleaf forest of Ailaoshan (ALS)

Variables	Forest Ecosystems	
	Subalpine coniferous forest in Lijiang (LJ)	Subtropical evergreen broadleaf forest in Ailaoshan (ALS)
Ecosystem Type	Subalpine coniferous forest ecosystem	Subtropical evergreen broadleaf forest ecosystem
Latitude and longitude	27°08′ N, 100°13′ E	24° 32'N, 101° 01'E
Elevation (m)	3240	2480
MAT (°C)	7.9	11.3
MAP (mm)	1587.5	1704.5
Soil Type	Loamy[a]	Loamy clay[f]
pH	4.4 to 4.9[a]	5.5 to 6[a]
SOC (mg kg^{-1})	74.09 ± 15.82	137.80 ± 74.37
TN (mg kg^{-1})	5.93 ± 1.03	9.22 ± 3.57
C/N ratio	12.43 ± 0.78	14.26 ± 2.08
Average Canopy Height (m)	38-42[a]	25-30[a]
Mean DBH of trees (mm)	59.4 [d]	50.3[d]
Basal area (m^2/ha)	27.69[d]	91[b]
Leaf area index (m^2/m^2)	~3	~5[c]
Tree Density (tree ha^{-1})	500[d]	1850[d]
Stand Age (years)	250–300	More than 300[e]
Litterfall (t ha^{-1})	5.11[a]	8.62[a]

Note MAT means mean annual temperature; MAP means mean annual precipitation; SOC means soil organic carbon; TN means total nitrogen; DBH means diameter at breast height. The references were cited from: a (Fei et al. 2018); b (Schaefer et al. 2009); c (Tan et al. 2011); d (Luo et al., 2017); e (Tan et al. 2013); f (Gong et al. 2011)

°C, and the distance from infrared light to ground is 1.7 m. The measurement time or closing period of each chamber is 5 min to measure soil CO_2 efflux. Data were collected at hourly intervals, as controlled by a data logger (CR-1000, Campbell Scientific Inc., Logan, UT, USA). Infrared light warming treatment is very useful for soil warming in forest ecosystems because no disturbance is made to the soil (Liang et al. 2003; Wu et al. 2016). For trenching treatments, a 1 m × 1 m square trench (width of 30 cm, depth of 50 cm) was dug to form a cube of soil contained by PVC planks; soil was backfilled by its original layers with topsoil over subsoil. The main components of the control box include an infrared gas analyzer (IRGA, Li-820, Li-Cor Inc., Lincoln, NE, USA) and a data logger (CR10X, Campbell Scientific Inc., Logan, UT, USA). Li-820 was calibrated regularly using standard gases. The maximum gas flow rate is 1 L/min, and the pressure compensation range is from 15 kPa to 115 kPa. The flow rate and airtightness checked regularly by site engineer. Trenching treatment with warming was applied by infrared light warming to measure heterotrophic respiration with warming (*Rhw*). *Ra* was calculated from the difference between *Rs* and *Rh*. *ST* at 5 cm depth and air temperature within each chamber were measured with homemade thermocouples (Tan et al. 2013). The soil water content at 10 cm depth was monitored with time-domain reflectometers (CS-616, Campbell Scientific Inc., Logan, UT, USA). Air pressure (*P*, *hPa*) at a 30-cm height in the center of the plot was measured by a pressure transducer (PX2760, Omega Engineering, Inc., Stamford, CT, USA). More detailed information on the method used is provided in (Liang et al. 2010; Tan et al. 2013).

2.3 Equations and Calculations

2.3.1 Soil CO_2 Efflux (*Rs*)

An automated chamber system for non-steady-state design with a flow-through was used to measure *Rs* at all observation times. Each chamber received 24 data points for *Rs* (hourly) and 48 data points for soil temperature at 5 cm and soil water content (0–10 cm) (twice per hour), except during periods of electrical failure. For each chamber, available data were used to calculate daily average values. The soil CO_2 efflux (*Rs*) was calculated as follows:

$$R_s = \mathrm{H}\frac{M}{V_0}\frac{P}{P_0}\frac{T_0}{T}\frac{dC_t}{dt} \quad (1)$$

where *Rs* is the soil CO_2 efflux ($\mu mol\ m^{-2}s^{-1}$); M is the CO_2 molar mass; P is pressure in Pascal (*Pa*); V_0, P_0 and T_0 are constants (22.4 $L\ mol^{-1}$, 1013.25 *hPa*, and 273.15 *K*, respectively); T is air temperature (*K*); H is the height of the respiration chamber (*m*); and dc/dt is the slope of CO_2 concentration variation with time over the measurement period.

2.3.2 Q_{10}

For the calculation of the temperature sensitivity of soil respiration, we used the exponential growth equation. An exponential model was used to examine the responses of *Rs* to *ST* (Lloyd and Taylor, 1994):

$$R_s = ae^{bT} \quad (2)$$

where a is basal respiration, b is the temperature sensitivity parameter, and T is soil temperature (°*C*) at a depth of 5 cm. Temperature sensitivity (Q_{10}, which describes the change in *Rs* for each 10 °C increase in soil temperature) for each chamber was calculated as follows:

$$Q_{10} = e^{10b} \quad (3)$$

2.3.3 Soil Warming Effect on Heterotrophic Respiration (*RhWE*), Soil Temperature and Soil Moisture

$$\text{Warming effect of heterotrophic respiration (\%)} = \frac{Rhw - Rh}{Rh} * 100 \quad (4)$$

where *Rhw* is heterotrophic respiration from the warming treatment and *Rh* is heterotrophic respiration from the trenching treatment.

The calculation of the soil warming effect on *ST* and *SM* is the same as that illustrated in Eq. 4.

2.4 Statistical Analysis

For statistical significance, all differences in *Rs, Rh, Ra, ST*, and *SM* were tested by a general linear model for repeated measurements. The mean value of Q_{10} for each treatment was tested by one-way ANOVA. Variations in *Ra, Ra: Rh, RhWE, RhWE%*, the increment of soil temperature caused by soil warming *(TWE)*,the incremental percentage of soil temperature caused by soil warming *(TWE%)*, and *SM* among treatments between LJ and ALS were tested by paired t tests. Independent samples t tests were used for Q_{10} comparisons between treatments and sites. Exponential regressions were used for the correlation between *ST* and *Rs* and its fractions. Then, the stepwise linear regression also performed for the increment value and percent (%) of *Rh* to soil warming for two ecosystems. All statistics were calculated in SPSS 16.0. All figures were completed using SigmaPlot 12.5 (Systat Software, San Jose, CA, USA).

3 Results

3.1 Soil Temperature and Moisture in Subalpine Coniferous Forests of Lijiang and Subtropical Forests of Ailao Mountain

The annual *ST* of LJ (7.76 ± 4.16 ℃) is less than that of ALS (11. 12 ± 3.41 ℃) (Fig. 1a, b). Soil warming significantly increased *ST* in LJ (10. 46 ± 4.01 °C, $p < 0.0001$) and ALS (13. 67 ± 3.23 ℃, $p < 0.0001$). The increase in *ST* decreased with increasing air temperature and was lower during the rainy season (LJ, 29.34 ± 7.25%; ALS, 17.15 ± 2.20%) than the dry season (LJ, 114.26 ± 74.82%; ALS, 36.99 ± 9.78%) at both research sites (Fig. 1a, b). NR did not affect *ST* significantly at either site.

The annual *SM* of LJ (45.54 ± 0.16%, F = 11.172, $p < 0.0001$) was higher than that of ALS (33.40 ± 0.13%, F = 7.187, $p < 0.0001$) (Fig. 1c, d). The seasonal dynamics of *SM* of CK and NR, and root trench settings followed the same trend, with levels being higher in the rainy season (from July to September) and lower in the dry season (from April to May). The annual *SM* levels was significantly higher in NR (LJ, 47.86 ± 5.97%; ALS, 40.90 ± 5.34%) than in NRW (LJ, 44.23 ± 8.84%; ALS, 36.99 ± 3.05%) and CK (LJ, 43.22 ± 9.22%; ALS, 34.97 ± 5.21%) at both research sites (Fig. 1c, d). During the rainy and dry seasons, firstly *SM* was highest in NR, followed by NRW and by CK respectively. The significant differences in *SM* between CK and NRW and NR and NRW were observed only during the dry season ($p < 0.0001$) in LJ and ALS (Fig. 1, S1).

Compared to CK, the annual increment of *SM* for NR was greater for ALS (ALS, 17.27 ± 5.48%, LJ, 16.47 ± 7.36%; t = 1.861, df = 270, $p = 0.064$) than for LJ (Figure S1a). Compared to NR, the decreasing ratio of soil warming to *SM* was significantly lower for ALS (-9.02 ± 6.26%) than for LJ (-9.39 ± 9.29%) (t = 2.362, df = 270, $p = 0.019$) (Figure S1). NRW increased *SM* compared to CK, and the increase for ALS (6.59 ± 7.79%) was 1.95 times that of LJ (3.38 ± 8.89%) (t = 5.54, df = 270, $p < 0.0001$) (Figure S1b).

3.2 Soil Respiration of Subalpine Coniferous Forests of Lijiang and Subtropical Forests of Ailao Mountain

The seasonal dynamics of *Rs* (LJ, F = 48.33, $p < 0.0001$; ALS, F = 48.33, $p = 0.001$), Rh (LJ, F = 25.71, $p < 0.0001$; ALS, F = 25.71, $p = 0.006$) and Ra (LJ, F = 17.83, $p < 0.0001$; ALS, F = 87.97, $p < 0.0001$) were significantly stronger in the rainy season than in the dry season in LJ and ALS (Fig. 2a, b). *Rs, Rh* and *Ra* were stronger in ALS than LJ during the observation period (Fig. 2).

The trenching effect of *Rh* in LJ was higher than in ALS but the warming effect of *Rh* in LJ was lower than in ALS annually (Figure S2). Hence, the trenching plus warming effect of *Rh* in LJ was higher than in ALS for all seasons in Figure S2.

Furthermore, the inner annual dynamics of the ratios of *Rh: Rs, Ra: Rs*, and *Ra: Rh* were significant, but there were no clear trends for ALS and LJ (Fig. 2c, d). The ratio of *Rh* to *Rs* was significantly higher in the in LJ (0.84 ± 0.03) than in ALS (0.76 ± 0.06) (t = 19.15, df = 349, $p < 0.0001$). The ratio of *Ra* to *Rh* was significantly lower in LJ (0.20 ± 0.04) than in ALS (0.33 ± 0.13) during the observation period (Fig. 2, S3).

3.3 Soil Temperature and Moisture Effect on Soil Respiration Fractions in Subalpine Coniferous Forests of Lijiang and Subtropical Forests of Ailao Mountain

According to Pearson correlation analysis results, *Rs, Rh* and *Ra* had a significant positive correlation with *ST* and *SM*, but the correlation with *ST* was stronger than that with

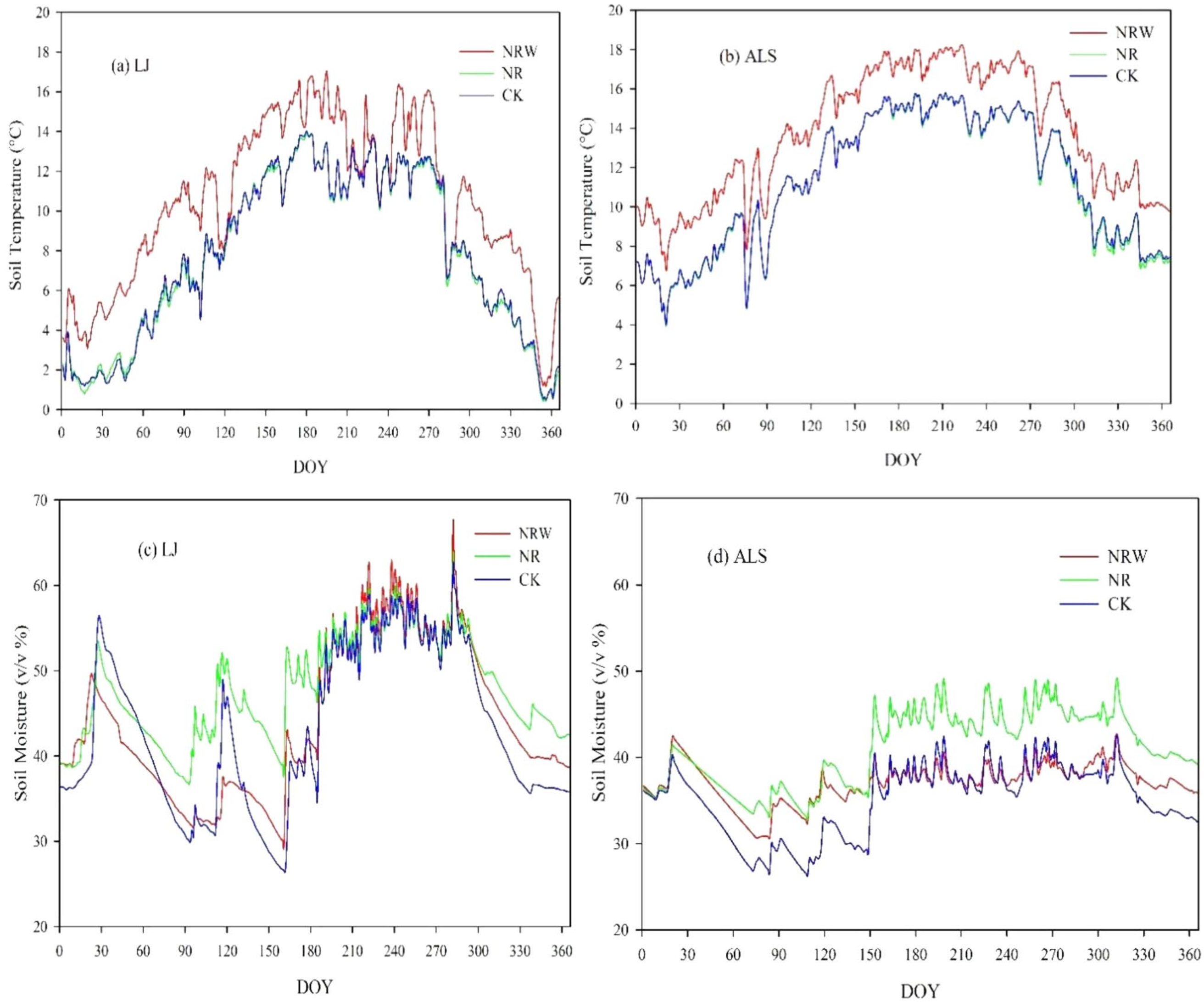

Fig. 1 (**a**, **b**) Daily average soil temperature and (**c**, **d**) daily average soil moisture for subalpine coniferous forest in Lijiang (LJ) and subtropical forest in Ailao Mountain (ALS). Remark: CK denotes the control treatment; NR denotes the trenching treatment; NRW denotes the trenching treatment with warming and DOY denotes date of year

SM in LJ and ALS (Table 2). According to the nonlinear regression wizard, *ST* and *SM* values attributed to *Rs* and *Ra* were more common in ALS than in LJ, but *Rh* was higher in the LJ than in ALS (Fig. 3a-f).

The correlation between the ratio of *Rs* and *SM* and *ST* was significant, and echoing the relationship between *Rs* and *SM* and *ST* in LJ (Table 2). Only *Ra*: *Rh* was negatively correlated with the *ST* of NR in LJ. SM and ST explained the ratios of Rs significantly with a lower explain rate found for LJ (Fig. 3). Q_{10} was not significantly different between *Rs*, *Rh* and *Ra* in LJ (Fig. 4a). However, the Q_{10} of *Ra* was significantly lower than that of *Rs* and *Rh* in ALS (Fig. 4b).

3.4 Warming Effect on Soil Heterotrophic Respiration in Subalpine Coniferous Forests of Lijiang and Subtropical Forests of Ailao Mountain

In the NRW treatment, the seasonal dynamics of *Rs* were significantly higher in the rainy season and lower in the dry season (Fig. 5). *RhWE* and the percent increase were greater during the dry season than during the rainy season at both sites. The percent increase was significantly greater in LJ (62.14 ± 21.22%) than in ALS (38.64 ± 27.69%) during the observed period (Fig. 5).

Similar to *Rh, Rhw* was better correlated with *ST* than *SM* in ALS and LJ. Compared to the NR treatment, Q_{10} decreased in the NRW treatment at both sites. The reduction

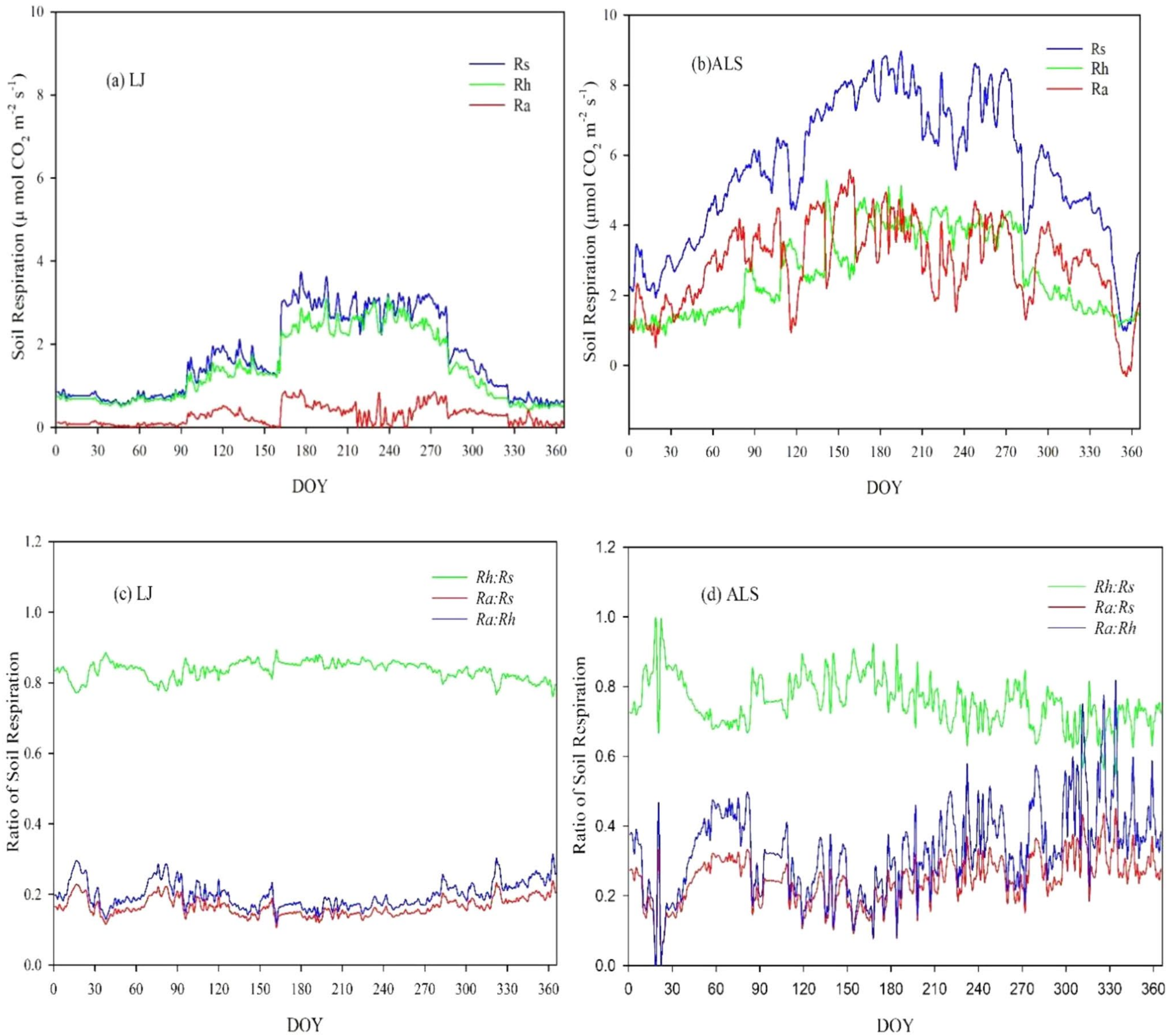

Fig. 2 (**a**, **b**) Soil respiration (*Rs, Rh, Ra*) and (**c, d**) ratios (*Rh: Rs, Ra: Rs and Ra: Rh*) for subalpine coniferous forest in Lijiang (LJ) and subtropical forest in Ailao Mountain (ALS). Remark: *Rs* denotes total soil respiration; *Rh* denotes heterotrophic respiration; *Ra* denotes autotrophic respiration; *Rh: Rs* denotes the ratio of heterotrophic respiration to total soil respiration; *Ra: Rs* denotes the ratio of autotrophic respiration to total soil respiration; *Ra: Rh* denotes the ratio of autotrophic respiration to heterotrophic respiration and DOY denotes date of year

in Q_{10} was greater in ALS (ALS 18.5%; LJ 2.03%) than in LJ (Fig. 4).

Rhw was significantly positively correlated with *ST* and *SM* (Table 2) in ALS and LJ. According to Equation $Y = a*e\ (b^{T})\ *SM^{c}$ (*T* is soil temperature, and *SM* is soil moisture), *ST* and *SM* explained 90.2% and 85.4% of *Rhw* in LJ and ALS, respectively.

The linear stepwise regressions show that the soil warming increment value and increment percent of *Rh* were driven by different factors at the two sites (Table 3). The *SM* of the trench treatment (SM_{NR}) ($R^2 = 0.45$) and soil trench and warming treatment (T_{NRW}) ($R^2 = 0.81$) was the main contributor the soil warming increment value of *Rh* for ALS and LJ, respectively. For *RhWE*, the difference in *ST* and *SM* between NR and NRW conditions was the main factor ($R^2 = 0.35$) together with $T_{NRW,}T_{WE}$ and M_{NR}, which explained 57% of the variance in ALS. In LJ, the *SM* of NR and NRW together explained 99% of the variation in *RhWE*.

Table 2 Pearson correlation between soil respirations, its ratios, soil temperature and moisture of subalpine coniferous forest in Lijiang (LJ) and subtropical forest in Ailao Mountain (ALS)

Sites	LJ						ALS					
Treatment	Control		Root trench		Root trench + Warming		Control		Root trench		Root trench + Warming	
Parameters	*ST*	*SM*	*ST*	*SM*	*ST*	*SM*	*ST*	*SM*	*ST*	*SM*	*ST*	*SM*
Rs	0.870**	0.701**					0.956**	0.502**				
Ra	0.589**	0.467**					0.775**	0.433**				
Rh			0.889**	0.594**					0.929**	0.630**		
Rh: Rs	0.571**	0.304**	0.571**	0.304**				0.126*				
Ra: Rs	−0.571**	−0.304**	−0.571**	−0.304**								
Ra: Rh	−0.570**	−0.303**	−0.570**	−0.303**					−0.113*			
Rhw					0.814**	0.659**					0.895**	0.470**

** The significance level is 0.05

Remark: Rs, total soil respiration; Ra, autotrophic respiration; Rh, heterotrophic respiration; Rh: Rs, the ratio of heterotrophic respiration to soil respiration; Ra: Rs, the ratio of autotrophic respiration to soil respiration; Ra: Rh, the ratio of autotrophic respiration to heterotrophic respiration; Rhw, heterotrophic respiration in the trench and warming treatment; LJ, subalpine coniferous forest on Yulong Snow Mountain of Lijiang; ALS, subtropical evergreen broadleaf forest on Ailao Mountain; ST, soil temperature; SM, soil moisture

4 Discussion

It has long been identified that *ST* and *SM* are the main controlling factors of *Rs* in terrestrial forest ecosystems and fundamental parameters in predicting *Rs* responses to global change (Xia et al., 2009). Moreover, *ST, SM* (Eliasson et al. 2005; Li et al. 2017) and nutrient availability (Eliasson et al. 2005) are the primary abiotic influencing factors for the regulation and variation of *Rs* and its fractions. In this study, LJ and ALS showed that *ST* is the most important factor controlling *Rs, Rh* and *Ra* because these forest ecosystems are not water-limited ecosystems that cannot constitute a significant portion of the global Ccycle (Zhang et al. 2015). Generally, higher *Rh* carried higher soil microbe activity seeing that higher soil microbial activity belongs to high soil carbon(C): nitrogen (N) ratio. In this study, soil C: N ratio of ALS was higher than in LJ. Normally, *ST* and *SM* have direct effects on changes in the activities of root and soil microbial activities (Li et al. 2017), which leads to *ST* and *SM* being the most important factors of *Rs* (Han et al. 2019; Mukhortova et al. 2021).

However, *Ra* was influenced by so many climatic and edaphic drivers in regional and global scales (Tang et al. 2020). Hence, net ecosystem exchange (NEE) or one of the climatic and edaphic drivers in ALS was higher than in LJ (Fei et al. 2018), seeing that higher root biomass leads to higher *Ra*, but NEE does not lead it directly. Accordingly, subtropical evergreen forest dominates the evergreen broad leaf, has a more diverse species composition and more root biomass (Hu et al. 2022) than subalpine coniferous forest, contributing to increased *Ra* levels on ALS than on LJ. Additionally, fine roots with a short lifespan and fast turnover rate absorb a large amount of water and nutrients and carry out C and N cycling to ensure plant photosynthesis, growth, and maintenance (Li et al. 2022). The C fraction of fine roots in broadleaf forests is higher than that in coniferous forests (Neumann et al. 2020).While *Ra* varies considerably across terrestrial ecosystems, broad-leaf forests have the highest *Ra* values, needle-leaf forests have the lowest *Ra* values, and tropical forests have the highest and lowest values in boreal forests (Tang et al. 2020). However, this study shows that the *Ra* of subtropical evergreen broad leaf forest is higher than that of tropical rainforest in Xishuangbanna (XSBN) (Lu et al. 2009). As most *Ra* comes from fine roots, the most important reason is that the lesser root biomass in XSBN caused *Ra* to be lower than that at ALS. The higher clay content (19.5% in XSBN and 5–10% in ALS), (Yuan et al. 2022; Zhou et al. 2021b) and higher soil bulk density (BD) levels (1.3 g cm^{-3} in XSBN and 0.48 g cm^{-3} in ALS, (Qi et al. 2012; Zhou et al. 2021b) also contribute to the lower *Ra* of tropical rainforests. The *Ra* of subalpine coniferous forest in LJ is less than that in ALS and XSBN,

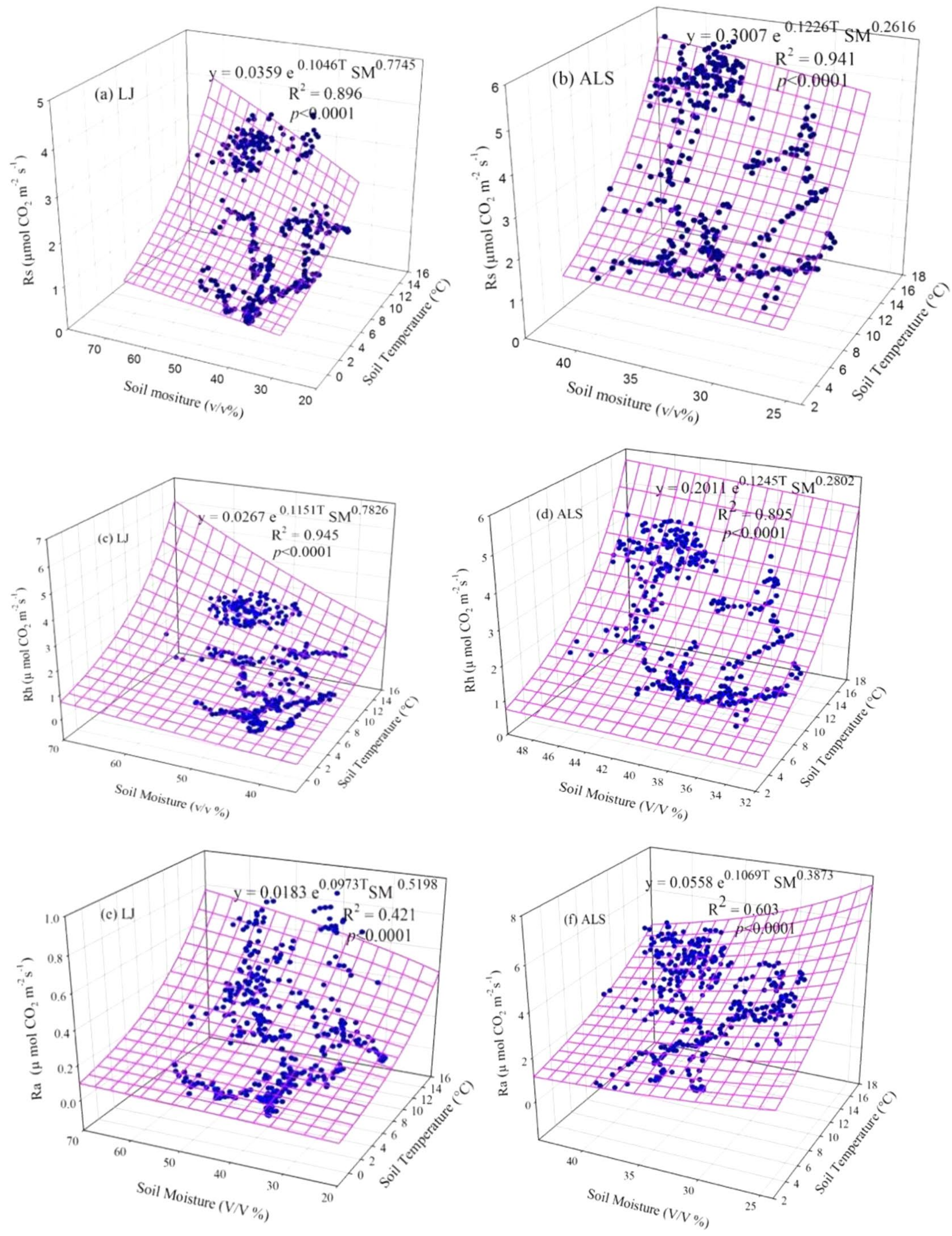

Fig. 3 (**a**, **b**) Regression analysis between soil temperature, soil moisture and total soil respiration(*Rs*), (**c**, **d**) regression analysis between soil temperature, soil moisture and heterotrophic respiration(*Rh*), and (**e**, **f**) regression analysis between soil temperature, soil moisture and autotrophic respiration (*Ra*) for subalpine coniferous forest in Lijiang (LJ) and subtropical forest in Ailao Mountain (ALS). Remarks: *Rs* denotes total soil respiration; *Rh* denotes heterotrophic respiration; *Ra* denotes autotrophic respiration; *ST or T* denotes soil temperature; and *SM* denotes soil moisture

corroborating the trend whereby *Ra* significantly increased with soil BD and total Rs but declined with increasing silt content, clay content and elevation (Chen et al. 2014) and gross primary production (GPP), ecosystem respiration (ER), net ecosystem production (NEP), belowground net primary production (BNPP), total belowground carbon allocation (TBCA), and leaf area index (LAI) (Tang et al. 2020). These factors affected *Rs* together, leading to the highest *Rs* levels in the subtropical evergreen forest. Therefore, the *Rh* contribution to *Ra* is greater in ALS than in LJ, and similar

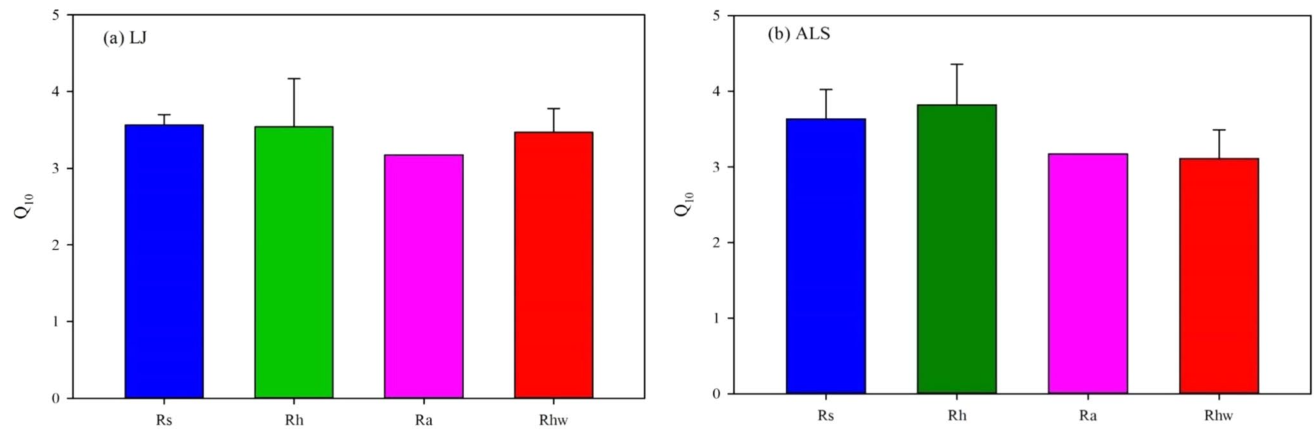

Fig. 4 (**a**) Q_{10} of *Rs, Rh, R*a, and *Rhw* for subalpine coniferous forest in Lijiang (LJ), and (**b**) Q_{10} of *Rs, Rh, R*a, and *Rhw* for subtropical forest in Ailao Mountain (ALS). Remarks: Q_{10} denotes temperature sensitivity to soil respiration; *Rs* denotes total soil respiration; *Rh* denotes heterotrophic respiration; *Ra* denotes autotrophic respiration; and *Rhw* denotes heterotrophic respiration with warming

to that in XSBN (29%) (Lu et al. 2009). Liang et al. 2017 reported that *Rh* contributed approximately 70% to *Rs* and that *Ra* contributed 30% to *Rs*. Another previous study found that *Rh* made 10–90% contributions to *Rs* in different forest ecosystems (Tang et al. 2019), and the present study also followed these ratios of contributions.

Moreover, *Rh*, the most important fraction of *Rs* is shaped by the soil microbe decomposed SOM rate (Han et al. 2019), which is the rate related to *ST* and *SM* when the soil microbe activity substrate is sufficient. *Rh* originates from trench treatment with higher SOM and without affected roots. As *Rh* contributed more in LJ than on ALS, it is more related to *ST* and *SM*. Otherwise, the greater variation in *SM* at LJ also led to *ST* and *SM* explaining more of the *Rh* in LJ (94.5%) than on ALS (89.5%). This finding also confirms that the global pattern of *Ra*-dominated factors is correlated with vegetation, temperature and precipitation (Tang et al. 2020). It is possible that influencing factors such as *ST, SM*, biological activities, vegetation patterns and distinct characteristics of soils are not uniformly affected and vary both spatially and temporally (Rasidah et al. 2003). Although, the responses of *Rh* to warming may vary in magnitude and even direction (Eliasson et al. 2005). Currently, global *Rs* is increasing, which will stimulate the degree of climate change, especially in terms of C losses from soils as a result of *Rh*, which remains highly uncertain (Bond-Lamberty et al. 2018).

Furthermore, Q_{10} varies across different ecosystems, as *Rs* shows seasonal variations and different temperature sensitivities (Epron 2010). The Q_{10} value increased while the temperature decreased(Li et al. 2020) and was found to be between 1.0 and 5.0 in many terrestrial ecosystems (Zou et al. 2018), and values of Q_{10} in the two study sites were also within this range. Although global Q_{10} data for *Rs* range from 1.3 to 3.3 (Aguilos et al. 2013), Q_{10} in this study was found to exceed this range. Additionally, $Q_{10}$was found to range from 2.3 to 6.21 for pine plantations (Luan et al. 2013), 1.7 to 5.12 for oak forests (Luan et al. 2013), 2.25 to 2.31 for temperate forests in Poland(Klimek et al. 2021) and 3.4 to 5.6 for beech forests in the United States (Yang et al., 2022). The Q_{10} of evergreen broadleaved forest is significantly lower than that of evergreen coniferous forest and deciduous coniferous forest (Xu et al. 2015). Little difference in the significance of the Q_{10} values between the two sites was found. It is possible that temperature control over soil C turnover is more sensitive in cooler climates than in warmer climates(Zou et al. 2018) or that Q_{10} does not vary considerably despite substantial differences in soil properties and respiration rates between forest types (Klimek et al. 2021). When Q_{10} was greater than 2.5, the mysterious process of substrate supply was generally confounded with the observed variation in temperature (Jia and Zhou 2009). Q_{10} of *Rs* and *Rh* includes direct and indirect effects related to the physiology of roots, the phenology of photosynthesis and C allocation to roots (Davidson et al. 1998). Thus, even the Q_{10} of *Ra* was similar to that of *Rs* and *Rh*, which does not indicate that *Rs* and its fraction responded to climate change at the same rate at ALS and LJ. Additionally, the values of Q_{10} vary over time and depend on the given region and ecosystem type (Lai et al. 2012). Furthermore, the Q_{10} decrement was greater for ALS than in LJ, which was due to the higher SOC content of ALS than in LJ, and SOC exhibited strong predictive power in predicting the Q_{10} value in tropical and subtropical forests; in contrast, the effect of SOC on the Q_{10} value was very weak in temperate and boreal forests (Li et al. 2020).

Furthermore, the warming effect on *Ra* was not statistically detectable during early warming years; in contrast,

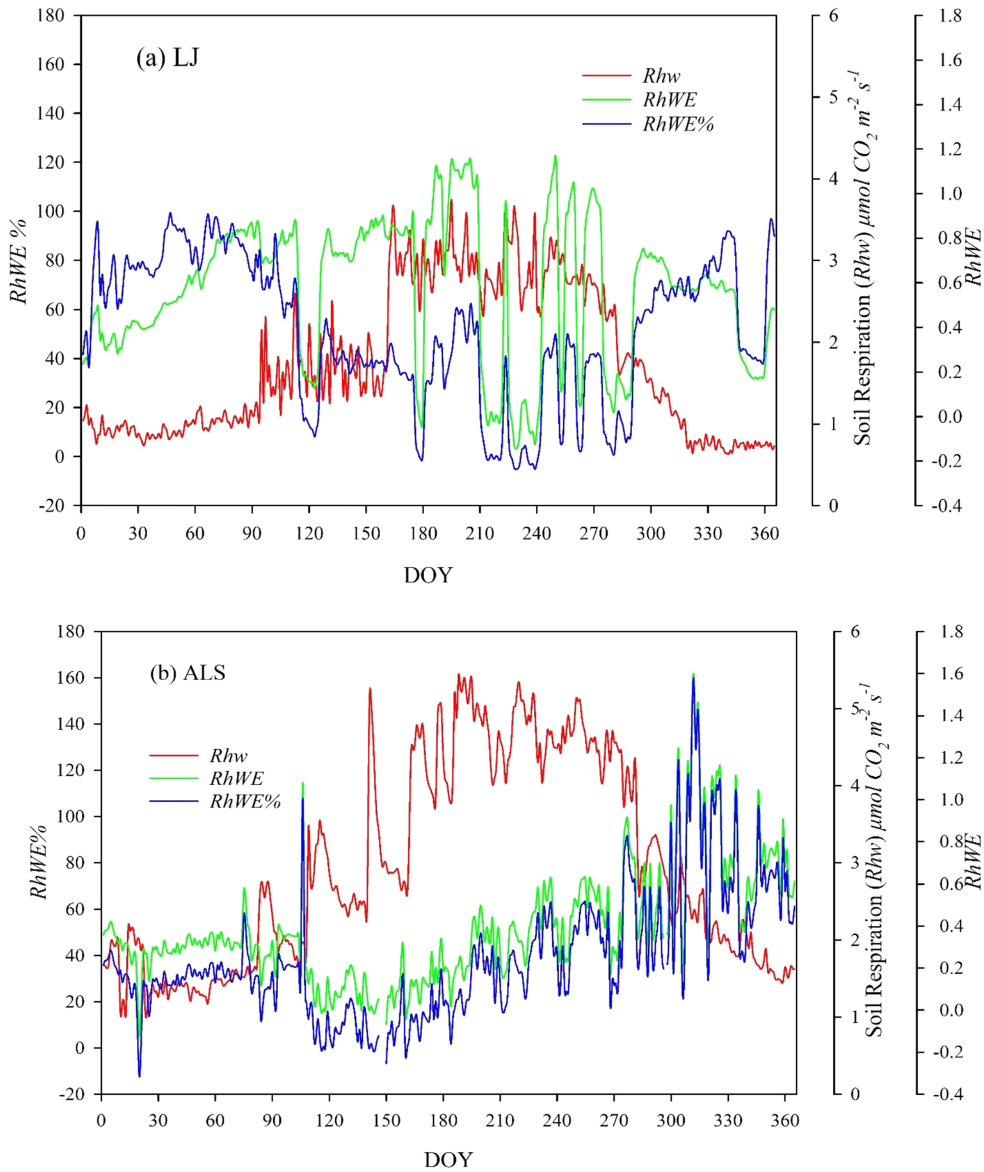

Fig. 5 Warming effect on soil heterotrophic respiration (**a**) in subalpine coniferous forest in Lijiang (LJ) and (**b**) in the subtropical forest of Ailao Mountain (ALS). Remarks: *Rhw* denotes heterotrophic respiration with warming; *RhWE* denotes the soil heterotrophic respiration incremental effect by soil warming; and *RhWE* (%) denotes the soil heterotrophic respiration incremental effect by soil warming as a percentage and DOY denotes date of year

warming by 2 °C increased *Rh* by an average of 21%, and this stimulation remained stable over the warming period (Wang et al. 2014). Then, warming decreased *SM* that warming can cause greater evapotranspiration (Yu et al. 2020). In addition, decreases in soil enzyme pools and their activity under warming may also contribute to a reduction in *Rh* (Yu et al. 2020).Hence, increasing *ST* accelerates organic matter decomposition rates and leads to a loss of soil C, which leads to a decrease in the soil C stock (Bao et al. 2016; Cheng et al. 2011; Giardina and Ryan 2000; Hopkins et al. 2014). The changes in *ST* and *SM* alter the activities of soil microorganisms and contingent effects by changing substrate supply and plant growth in forest ecosystems (Chen et al. 2017). These factors contribute to the soil warming effect on *Rh*, and the percent increase was significantly higher in LJ than in ALS. As increases in *ST* and decreases in *SM* induced by warming affect soil microorganisms, *Rs* is more sensitive to warming at lower temperatures (Kirschbaum 2006). Thus, the greater increases in *ST* and *SM* also caused *Rh* to increase more in LJ than on ALS that the soil warming effect on *Rh* may be greater where *ST* is lower (Schindlbacher et al. 2012; Yuan et al. 2019). The *ST*-increase experiments confirm that warming caused significant C losses from the soil not only in subalpine coniferous forests but also in subtropical forests in this study. This indicates that under climate warming, when precipitation is decreasing, soil C stock will be lower in much colder regions and loss rate much be higher in colder regions. Therefore, determining how to protect soil C under climate change in the future is an important issue.

As soil properties and plant and climate characteristics differ between ALS and LJ, the soil warming effect and

Table 3 Stepwise linear regression for the increment value and percent (%) of soil heterotrophic respiration to soil warming for subalpine coniferous forest in Lijiang (LJ) and subtropical forest in Ailao Mountain (ALS)

Sites	Parameters	Equation	Adj R^2	F	P
Subalpine coniferous forest in Lijiang (LJ)	increment value ($\mu molCO_2m^{-2}s^{-1}$)	$0.19+0.049T_{NRW}$	0.81	1236.00	$p<0.0001$
		$-0.23+0.047T_{NRW}+0.126T_{WED}$	0.94	2356.00	$p<0.0001$
		$-0.33+0.047T_{NRW}+0.13T_{WED}+0.0020SM_{NRW}$	0.95	1769.00	$p<0.0001$
		$-0.22+0.049T_{NRW}+0.13T_{WED}+0.0050SW_{NRW}-0.0050SM_{NR}$	0.95	1416.00	$p<0.0001$
	increment percent %	$92.35-4.13T_{NR}$	0.66	554.45	$p<0.0001$
		$25.86-22.98T_{NR}+19.10T_{NRW}$	0.99	48870.00	$p<0.0001$
		$27.38-22.93T_{NR}+19.06T_{NRW}-0.035SM_{NRW}$	0.99	34500.00	$p<0.0001$
		$26.38-22.86T_{NR}+19.08T_{NRW}-0.040SM_{NRW}+0.0062T_{WE}$	0.99	27560.00	$p<0.0001$
		$26.89-22.75T_{NR}+18.99T_{NRW}-SM_{NRW}+0.0067T_{WE}-0.032SM_{WE}$	0.99	23640.00	$p<0.0001$
Subtropical forest in Ailao Mountain (ALS)	increment value ($\mu molCO_2m^{-2}s^{-1}$)	$-2.90+0.092SM_{NR}$	0.45	283.24	$p<0.0001$
		$-4.63+0.10SM_{NR}+0.70T_D$	0.48	160.78	$p<0.0001$
		$-3.50+0.15SM_{NR}+0.70T_D-0.10SM_{NRW}$	0.53	132.09	$p<0.0001$
		$-4.69+0.13SM_{NR}+1.16T_D-0.070SM_{NRW}-0.014T_{WE}$	0.54	105.06	$p<0.0001$
		$-2.93+0.15SM_{NR}+1.19T_D-0.075SM_{NRW}-0.040T_{WE}-T_{NRW}$	0.57	95.06	$p<0.0001$
	increment percent %	$-49.99+33.74T_D$	0.097	38.39	$p<0.0001$
		$-168.02+70.02T_D-5.81SM_D$	0.35	95.05	$p<0.0001$
		$6.24+28.88T_D-8.26SM_D-5.54T_{NRW}$	0.44	93.69	$p<0.0001$
		$91.43+58.91T_D-8.53SM_D-12.66T_{NRW}-2.47T_{WE}$	0.53	100.74	$p<0.0001$
		$3.82+68.70T_D-4.76SM_D-13.88T_{NRW}-3.08T_{WE}+2.69SM_{NR}$	0.57	93.70	$p<0.0001$

Note The increment value indicates the difference in heterotrophic respiration between the trench treatment and trench and warming treatment; Increment percent % = *(HRw-HR)/HR**100%

T: Soil temperature; *SM*: Soil moisture; NR: root trench treatment; T_D: the difference between soil temperature; SM_D: the difference between soil moisture; NRW: root trench + warming treatment; WED: the difference between NR and NRW; and WE: the percent increase caused by soil warming

percent increase are greater in LJ than on ALS. Even the degree to which the warming effect was negative for mean annual precipitation (MAP) and SOC varied between sites; thus, the higher *RhWE* was higher in LJ, which had less rainfall and SOC than ALS (Fei et al. 2018). The annual dynamics of *RhWE* were stronger in the rainy season and lower in the dry season, but there were contrasting dynamics at ALS, even though *Rhw* had the same dynamics, with higher values occurring in the rainy season and lower values occurring in the dry season. This may be because the main control factors of *RhWE* differed for ALS and LJ. And *SM* is lower and *ST* is higher than values in LJ, so *SM* decreased more on ALS in the dry season and less in the rainy season due to higher rainfall levels than in LJ, which led to more *SM* variation between NRW and NR on ALS than in LJ. This result indicates that *SM* was the most important factor and explained *RhWE* by 45% on ALS, while the *ST* of the NRW treatment was the most important factor, explaining *RhWE* variation by 81%. This was because *ST* was lower than 15°C and showed greater annual variation than for ALS. As the relative increase in enzyme activity diminishes as temperature increases (Peterson et al. 2007; Schipper et al. 2014), the macromolecular rate theory (MMRT) deduces that the heat capacity of enzyme-catalyzed reactions explains *Rs* in laboratory- and field-based observations of a relatively lower net increase rate at higher temperatures (Schipper et al. 2014; Zhang et al. 2021). *Rs* is more sensitive to rising temperatures in relatively cold regions than in relatively warm areas (Carey et al. 2016; Jian et al. 2018; Li et al. 2020). Because cold areas contain more than half of global soil C stores (FAO et al., 2012), with temperatures increasing in these regions and rainfall decreasing in the tropics (IPCC 2022), this will lead to C budget changes in the global C budget.

5 Conclusions

In conclusion, the result of this study affirms that subtropical evergreen broadleaf forests of Ailao Mountain exhibited a lower warming effect on heterotrophic respiration, but not in subalpine coniferous forests of Lijiang. This study also confirmed that soil respiration and its components had positive correlation with soil temperature and moisture for two ecosystems. The study asserted that soil warming increased soil temperature in subalpine coniferous forests and subtropical evergreen broadleaf forests. The soil warming experiment can evaluate the impact of warming on soil respiration and its components, and the sensitivity of soil temperature and moisture in diverse ecosystems, especially for subalpine coniferous forests and subtropical evergreen broadleaf forests. The temperature sensitivity of autotrophic respiration was lower for two ecosystems than the temperature sensitivity of soil respiration and heterotrophic respiration in this study. The findings of this study have important implications for our understanding of the contribution of soil respiration to global carbon cycling in forest ecosystems under climate warming. This study provided to illustrate a privileged way for further observations and investigations to gain more insights on global carbon cycle. Further observations and investigations are necessary to improve our predictions of soil respiration and to assess the consequences of global climate change.

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Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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