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ORIGINAL PAPER

Response of soil respiration to environmental and photosynthetic factors in different subalpine forest-cover types in a loess alpine hilly region

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Abstract Soil respiration (R_s) is important for transporting or fixing carbon dioxide from the atmosphere, and even diminutive variations can profoundly influence the carbon cycle. However, the R_s dynamics in a loess alpine hilly region with representative sensitivity to climate change and fragile ecology remains poorly understood. This study investigated the correlation and degree of control between R_s and its photosynthetic and environmental factors in five subalpine forest cover types. We examined the correlations between R_s and variables temperature (T_{10}) and soil moisture content at 10 cm depth (W_{10}), net photosynthetic rate (P_n) and soil properties to establish multiple models, and the variables were measured for diurnal and monthly variations from September 2018 to August 2019. The results showed that soil physical factors are not the main drivers of R_s dynamics at the diel scale; however, the trend in the monthly variation in R_s was consistent with that of T_{10} and P_n. Further, R_s was significantly affected by pH, providing further evidence that coniferous forest leaves contribute to soil acidification, thus reducing R_s. Significant exponential and linear correlations were established between R_s and T_{10} and W_{10}, respectively, and R_s was positively correlated with P_n. Accordingly, we established a two-factor model and a three-factor model, and the correlation coefficients (R^2) was improved to different degrees compared with models based only on T_{10} and W_{10}. Moreover, temperature sensitivity (Q_{10}) was the highest in the secondary forest and lowest in the *Larix principis-rupprechtii* forest. Our findings suggest that the control of R_s by the environment (moisture and temperature) and photosynthesis, which are interactive or complementary effects, may influence spatial and temporal homeostasis in the region and showed that the models appropriately described the dynamic variation in R_s and the carbon cycle in different forest covers. In addition, total phosphorus (TP) and total potassium (TK) significantly affected the dynamic changes in R_s. In summary, interannual and seasonal variations in forest R_s at multiple scales and the response forces of related ecophysiological factors, especially the interactive driving effects of soil temperature, soil moisture and photosynthesis, were clarified, thus representing an important step in predicting the impact of climate change and formulating forest carbon management policies.

Keywords Loess alpine hilly region · Soil respiration · Environmental factor · Photosynthesis factor · Q_{10} · Two-factor model · Three-factor model

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Introduction

Climate warming from 1880 to 2012 has led to an 0.85 °C increase in the global mean temperatures on land and ocean surfaces (Zhou et al. 2018). Indeed, climate change has huge potential to damage plant growth, water storage, agricultural production and economic activities (Chesney et al. 2017) and exacerbate drought and ecological imbalances. CO_2 also can affect global temperature (Friedlingstein et al. 2014). Soil respiration (R_s) is important for transporting or fixing CO_2 in the atmosphere, which is one of the most important carbon fluxes (Wu et al. 2020; Raich et al. 2002). The global soil organic carbon (SOC) pool is approximately twice as large as the OC pool in atmospheric and terrestrial organisms and more than tenfold larger than that caused by human activity (e.g., fuels combustions) (Lal 2008; Hashimoto 2012; Chen et al. 2020). Small variations in R_s may profoundly influence the carbon cycle and thus affect regional and even global climates through a variety of feedback processes. A potential positive feedback between warmer temperatures and intensive R_s could eventually accelerate global warming (Vargas et al. 2010a, b).

Therefore, information about R_s and its controlling environmental factors is of great significance in estimating the concentration of CO_2 in the atmosphere and its impact on global climate change, especially in response to the continuing trend in global warming trend. Monitoring soil temperatures in the field is an effective way to study the response of R_s to changes in soil temperature (Wertin et al. 2018) and provide a theoretical reference for probing the effects of long-term warming on soil C dynamics (Crowther et al. 2013). The R_s rates are dominated by soil temperatures (T_s) and soil moisture (SWC), which directly affect soil microorganisms and plant root activity and have indirect effects by changing substrate supply and plant growth (Hanson et al. 2000). A moderate temperature increase can accelerate soil humus decomposition and promote autotrophic respiration, thereby facilitating R_s activity. SWC, the main driver of net primary productivity, can intensely influence the input of C from litter and decompositions of soil organic matter, thereby affecting the output heterotrophic respiration and C output (Moyano et al. 2013). To date, the temperature sensitivity (Q_{10}) of R_s has been shown to decrease with increasing temperature and decreasing SWC (Flanagan and Johnson 2005). Other studies have shown that different forest types differ in the major factors that affect temporal and spatial variation in R_s, including soil temperature and moisture, root biomass, litter inputs, microbial populations, plant metabolism, other annually or seasonally fluctuating conditions and processes, and even plant phonological patterns (Curiel Yuste et al. 2010; Sheng et al. 2010; Zeng et al. 2014). R_s is also influenced by soil properties that can change soil microbial community composition (Landesman et al. 2014), including soil pH, total N, available P, and litter C (Gao et al. 2018; Feng et al. 2014).

Traditionally, the diurnal and seasonal variations in R_s have been expressed as empirical functions of Ts or SWC for various ecosystems (Heinemeyer et al. 2012). However, plant photosynthetic activity plays a significant role in regulating and forecasting R_s, especially in drylands (semiarid and arid areas), which have low levels of microbial activity and organic C in the soil; moreover, litter can lead to rhizosphere respiration becoming the dominant factor in R_s (Jia et al. 2018) because the source of C for the rhizosphere respiration of plants is provided by photosynthesis. Therefore, T_s and SWC may not fully represent R_s across multiple spatial and temporal scales. In addition, diurnal and weekly variation in R_s may be closely related to canopy photosynthesis, while the correlation between R_s and canopy photosynthesis (Hölttä 2010)under seasonal and interannual variation needs to be assessed by estimating productivity (Vargas et al. 2010a, b). However, due to the limitations of complex local geographical conditions and other problems, it is difficult to evaluate productivity using an eddy correlation system, a method to explore the annual variation law of R_s via single leaf photosynthesis (Wertin et al. 2018). In addition, after a large area of near-natural stand transformation occurs, ecosystems with the same stand type will appear as "fragmented" (large-scale pure forest planting area disappears and is replaced by other tree species), which adds to the difficulties and uncertainties in macroscopic analysis of the photosynthetic characteristics of different stand types. Consequently, it may be more accurate to assess the correlation by measuring the combination of single leaf photosynthesis with R_s.

The study site in the eastern part of the Qinghai-Tibet Plateau is representative of areas that are sensitive to climate change and of fragile, complex ecological environments with unique geographical features (Yao et al. 2005; Fu et al. 2006; Liu and Chen 2000). In recent years, arid and semiarid areas have been identified as potential C sinks (Ardö and Olsson 2003). However, as a major component of the semiarid and arid region, the response to the carbon cycle in various ecosystems under climate change in the Qinghai Tibet Plateau is poorly understood, especially in subalpine forest ecosystems (in contrast to the relatively well-studied R_s component in alpine, subalpine meadow and permafrost ecosystems) (Ren et al. 2017; Li et al. 2017; Peng et al. 2015). Forest R_s mainly emerges from the root system, microbial community and soil organic matter metabolism. The habitat provided by different forest stands determines which ecological and biophysiological factors lead to differences in R_s. Therefore, the annual and seasonal changes in remote sensing for specific types of subalpine forest ecosystems on the

Qinghai-Tibet Plateau, the response to relevant ecological and physiological factors, and the sensitivity to temperature need to be further explored and studied on a multispatial scale.

Hence, we established a fitting model between the R_s and the SWC, the T_s and combination of SWC and T_s to illustrate the interaction of temperature and moisture on R_s. Moreover, we introduce P_n as the main evaluation factor to establish a three-factor model to more comprehensively assess R_s regulation and response to various factors in this research area to provide direction and theoretical support for the study of R_s in typical stands of subalpine forest ecosystems in alpine hilly areas. The objectives were to (1) reveal any multitemporal scale changes in R_s in different forest covers; (2) test for a correlation between R_s and T_s, SWC and combination of T_s and SWC; (3) evaluate the effect of single leaf photosynthesis on R_s; (4) compare the adaptability of different forest covers to warming trends based on Q_{10}; and (5) investigate the correlation between R_s and other ecological environmental factors.

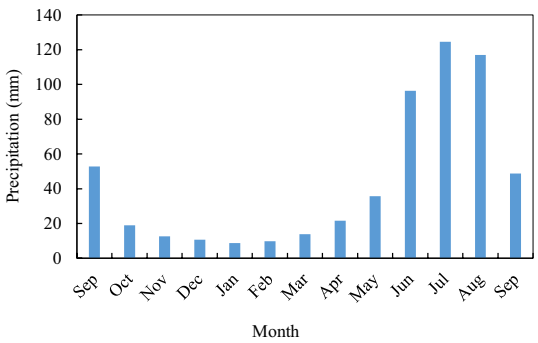


Fig. 1 Monthly variations in precipitation was presented from September 2018 to September 2019 in study site

Materials and methods

Study site

The research was carried out at the several forest reserves in Datong County (37°23′N, 101°51′E) in eastern Qinghai Province, including Tal Gou, Yang Jia Zhai, and An Men Tan. This region is the transition zone between the Qinghai-Tibet Plateau and the Loess Plateau, with an altitude of 2280–4622 m. Typical continental climate predominates in this area, with an annual mean temperature and relative humidity of 4.9 ℃ and 56%, respectively. The annual mean precipitation and evapotranspiration are 523.3 mm and 1762.8 mm, respectively. April to September (the plant growing season) is the rainy season in which 87% of the rainfall occurs, and the dry season is usually from November to March (Fig. 1). Major afforestation species include *Picea crassifolia* Kom., *Juniperus przewalskii* Kom., *Populus cathayana* Rehd., *Larix principis-rupprechtii* Mayr, *Betula platyphylla* Suk., and *Caragana korshinskii* Kom.

Experimental plots

Five representative forest covers containing secondary forest (S_1), *L. principis-rupprechtii* (S_2), *P. crassifolia* (S_3), *P. cathayana* (S_4) and *B. platyphylla* (S_5) plantations were chosen as experimental plots during the spring through early fall of 2018. All slope directions were shady, and slopes did not exceed 20°. The total number of plots (the fixed size was 20 × 20 m) was 15, which included three replicates (a similar plot was selected according to afforestation data from the local forestry bureau) per forest cover, and each plot was separated by a buffer of at least 20 m. Elevation, slope, tree height, diameter at breast height (DBH), forest age, stand density, canopy density and physical and chemical properties in the topsoil (0–20 cm) were measured for each plot (Tables 1, 2). The main vegetation types of secondary forest were *B. platyphylla*., *L. principis-rupprechtii*, *P. cathayana*, and *P. crassifolia* (not long after replanting, the forest age was 10 years) present at a ratio of 3:3:2:2.

Table 1 Main stand formation of experimental plots was measured in Loess alpine hilly region

Cover type	Elevation (m a.s.l.)	Slope (°)	Mean tree height (m)	Mean DBH (cm)	Mean forest age (year)	stand density (inds·ha^{-1})	Canopy density(%)
S_1	2960.3	14	9.45	12.89	22.4	1800	68
S_2	2910.4	13	12.23	15.46	25	2250	80
S_3	2919.7	15	13.02	14.25	25	2250	85
S_4	2863.6	17	10.34	20.65	30	2000	75
S_5	2876.4	18	10.85	14.47	23	2000	70

Notes S_1, S_2-S_5 refer to five representative forest covers containing secondary forest (S_1), *L. principis-rupprechtii* (S_2), *P. crassifolia* (S_3), *P. cathayana* (S_4) and *B. platyphylla* (S_5) plantations

Table 2 Main topsoil (0–20 cm) physical and chemical properties of experimental plots were measured in Loess alpine hilly region, and the observation of soil respiration was performed simultaneously

Cover type	Bulk density ($g \cdot cm^{-3}$)	pH	SOC ($g \cdot kg^{-1}$)	TN ($g \cdot kg^{-1}$)	TP ($g \cdot kg^{-1}$)	TK ($g \cdot kg^{-1}$)	Soil C:N ratio
S_1	0.98 ± 0.01c	8.11 ± 0.25a	23.98 ± 1.94a	2.65 ± 0.44a	0.72 ± 0.14a	0.63 ± 0.08a	9.49 ± 0.46b
S_2	1.08 ± 0.06a	7.53 ± 0.36c	21.61 ± 1.68b	2.13 ± 0.36c	0.44 ± 0.26c	0.36 ± 0.11d	8.07 ± 0.28d
S_3	1.06 ± 0.04a	7.30 ± 0.23d	18.34 ± 1.45d	1.87 ± 0.42d	0.57 ± 0.13b	0.52 ± 0.16bc	9.81 ± 0.42a
S_4	1.01 ± 0.03b	7.97 ± 0.35b	19.26 ± 1.52c	2.09 ± 0.35c	0.49 ± 0.12c	0.56 ± 0.15b	9.21 ± 0.97c
S_5	0.96 ± 0.03c	8.06 ± 0.24ab	17.18 ± 1.76d	2.25 ± 0.57b	0.62 ± 0.08ab	0.48 ± 0.09c	9.60 ± 13.53b

Notes S_1, S_2-S_5 refer to five representative forest covers containing secondary forest (S_1), *L. principis-rupprechtii* (S_2), *P. crassifolia* (S_3), *P. cathayana* (S_4) and *B. platyphylla* (S_5) plantations

Experimental design and measurements

Soil physicochemical properties

Measurements (total two) of all variables were completed in August 2019 according to government standards (Tables 1, 2). Five replicates per plot of undisturbed soil and the soil profile at 0–20 cm depth were collected with cutting rings, placed in separate sealed bags and brought to the laboratory to determine the physical properties of soil. Soil pH can be directly determined with a pH meter (Gao et al. 2018). Soil bulk density was determined using the method of White (1988). Soil samples were dried, ground, and sievied to determine the soil organic carbon (SOC), total nitrogen (TN), total phosphorus (TP), and total potassium (TK) contents as previously described (Clark et al. 1998; Mitchell et al. 1999; Udelhoven et al. 2003; West et al. 1989).

Soil respiration

From September 2018 to August 2019, in each plot, five PVC soil collars (20 cm in diameter × 10 cm in height) were randomly inserted to a 5 cm depth into the corresponding soil cores, which were extracted with a rubber hammer for R_s measurement. R_s was measured using a LI-8100 portable soil CO_2 flux system (LI-Cor Inc., Lincoln, NE, USA) (Xu et al. 2018), soil temperatures at a depth of 10 cm (T_{10}, °C) were measured with a thermocouple probe (LI-8100–201) connected to the LI-8100 system, and moisture in the 0–10 cm layer (W_{10}, % vol) near the collar was measured simultaneously with a time-domain reflectometry (TDR) probe (model TDR300, Spectrum Technologies, Plainfield, IL, USA) (Gao et al. 2018). All indicators were observed between 09:00 and 11:00 h at least every 2 weeks because of their accuracy in estimating the daily mean value (Xu and Qi 2001a). In addition, in October 2018 and January, April, and July 2019, we measured diurnal variation every 2 h from 09:00 h to 07:00 h the next day. The final calculated values reflected the average of 5 repeated measurements. Before sampling, the plants in the collars should be carefully removed.

Photosynthetic variables

P_n was determined for plants around each collar using a LI−COR 6400 photosynthesis system (LI−COR, Lincoln, USA) using randomly selected five fully expanded and representative upper leaves for broad-leaf species *P. cathayana* and *B. platyphylla* and a sprig with numerous leaves for coniferous species *L. principis-rupprechtii* and *P. crassifolia* at the same time as R_s was measured, including measurement of diurnal variations (daytime: 09:00–19:00 h). After each measurement, the leaf area in the chamber was estimated, and the gas exchange flux was modified accordingly. The leaf area of the plants to be measured was estimated using the leaf area index (LAI), which was determined using fixed points by a canopy analyzer and analyzed by WinSCANOPY2006a. The variation in P_n in S_1 was obtained by calculating the ratio of total net photosynthetic yield to the total leaf area of the canopy of different tree species in the sample plot.

Model calculation

To quantify the relationship between R_s, T_{10} and W_{10}, we established correlation models to analyze and compare the temperature sensitivity in different forest covers. The linear and nonlinear regression models were as follows:

$$R_s = ae^{bT_{10}} \tag{1}$$

$$R_s = aW_{10} + b \tag{2}$$

$$R_s = ae^{bT_{10}}W_{10}^c \tag{3}$$

where a, b and c are undetermined parameters. R_s is soil respiration.

Q_{10} was calculated by the following formula:

$$Q_{10} = e^{10b} \tag{4}$$

Data analyses

Data are represented as the means ± standard errors (SE). Means for each variable were analyzed using a one-way ANOVA, and significant differences among the means were tested by Duncan's multiple range test using a significance level of $\alpha = 0.05$ or 0.01 via SPSS 26.0 (IBM, Armonk, NY, USA). Means for several important parameters were tested for correlations using a Pearson correlation analysis. Simple linear regression analyses were used to examine the relationships between relative changes in R_s and Q_{10} values, and linear or nonlinear regression was used to evaluate the relationships between R_s and SOC, TN, TP, TK, soil C: N ratio, and P_n, which described the effects of biotic and abiotic factors on R_s. Results were plotted using Origin 2018 software (OriginLab, Massachusetts, USA).

Results

Diurnal variations in R_s and P_n

Maximum and minimum values for R_s were measured at 15:00 – 17:00 and 5:00 – 7:00, respectively (Fig. 2A). R_s of broad-leaf species was markedly higher than that of coniferous species during spring, summer, and autumn. Compared with the pure forest (S_2–S_5), the mixed secondary forest (S_1) had significantly higher values, except in winter ($p < 0.05$). During winter, no dramatic variation was detected in any forest covers ($p > 0.05$).

The diurnal variation in T_{10} in each stand did not significantly fluctuate, except in April, and the temperature was higher during the day than at night. Moreover, the amplitude of variation was marginal in W_{10}, with only a certain fluctuation in April and July (Fig. 2B, C). The variation in W_{10} was remarkable in S4 during summer.

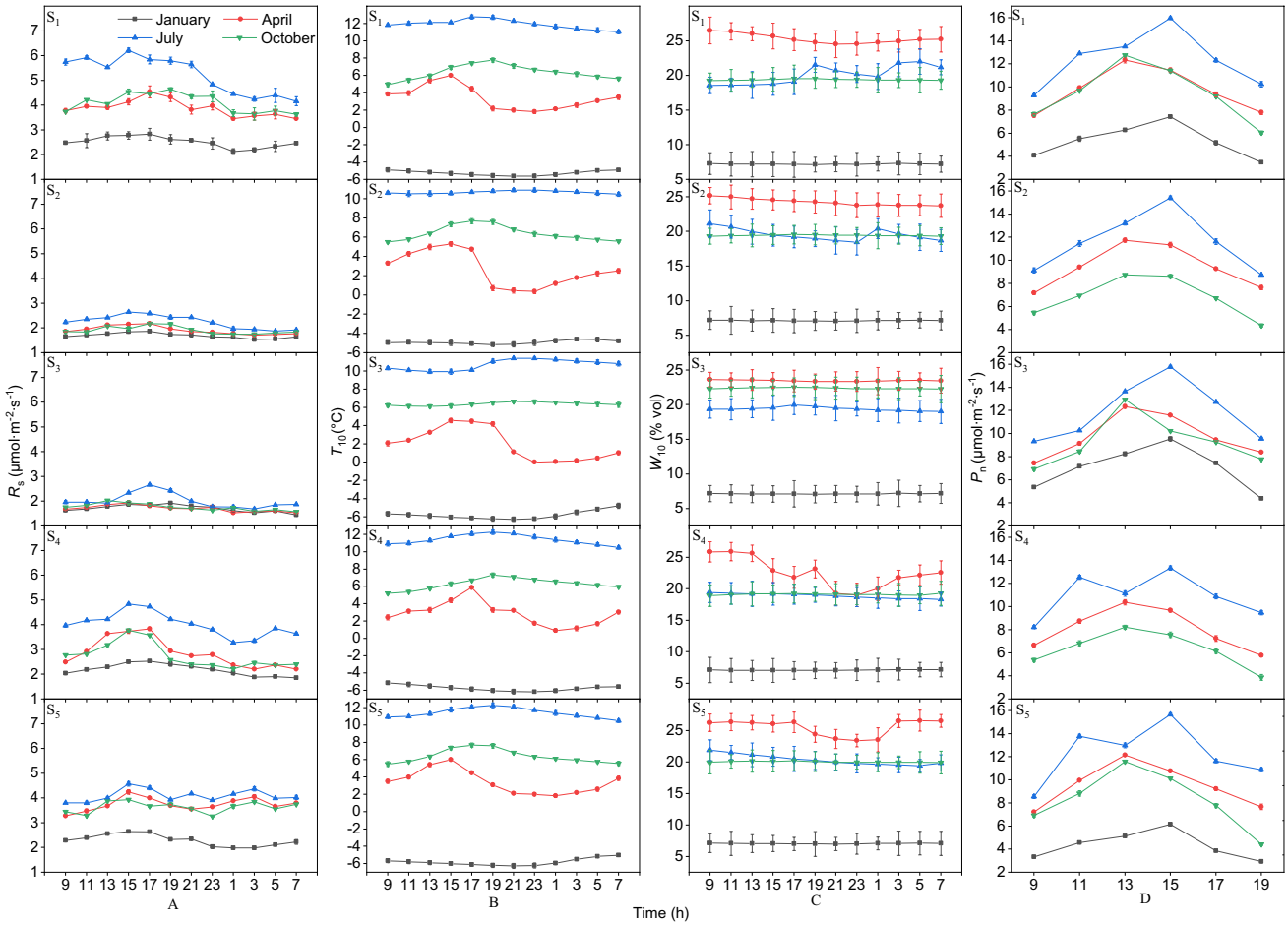


Fig. 2 Diurnal variations in (A) soil respiration (R_s), (B) soil temperature (T_{10}) and (C) soil moisture content (W_{10}) at 10 cm depth, and (D) net photosynthetic rate (P_n) for different forest covers: Secondary forest (S_1), *L. principis-rupprechtii* (S_2), *P. crassifolia* (S_3), *P. cathayana* (S_4), and *B. platyphylla* (S_5) plantations in October 2018 and January, April, and July 2019. Vertical bars represented the means ± SE

As shown in Fig. 2D, P. *cathayana.* and *L. principis-rupprechtii* were not measured in the winter, because the leaves had fallen off completely. The diurnal variations in P_n in the ved species emerged as a bimodal type, which was different from the unimodal type of coniferous species. Furthermore, no remarkable diurnal variations in P_n were demonstrated with the five forest covers during the winter, and only those of S_1 and S_3 represented a significant change.

Monthly variations in R_s, T_{10}, W_{10} and P_n

As shown in Fig. 3, the trend of T_{10} decreased from September to January and then rebounded until August; with the lowest values in January. The temperature range in this area is large, and reaches − 6.23 to −.94 in January and 12.07–3.15 in August. Overall, significant differences were not observed between the forest covers, except in January, July and August.

The W_{10} values were highest in April, fluctuated between May and August. During the spring and summer, the W_{10} values of forest covers represented extremely strong significance ($p < 0.01$). The seasonal coefficients of variation (CV) were 40.59%, 40.09%, 39.23%, 34.41%, and 36.54%, respectively, which demonstrated severe fluctuations in the water changes in the plantations of the five forest stands. In addition, the W_{10} of S4 was apparently lower than that of other forests during the growing season.

The trend of R_s changes with month was similar to that of T_{10}. The R_s readings of S_1 were markedly higher than those of the other forest stands, while no significant difference was observed between S_2 and S_3. During the nongrowing season (from October to March in the study site), the R_s values of *P. cathayana.* plantations were dramatically lower than the others. The CV was 26.86%, 15.59%, 13.94%, 26.51%, and 21.94% for $S_1 - S_5$.

The variation regulation of P_n was similar to that of R_s throughout the year, except for the values in S_3, which were significantly higher than those of S_1 and S_5 during the winter. The P_n of S_4 was significantly lower than that of the others, and no conspicuous difference was exhibited between S_1 and S_5.

Fitting relationship between the R_s and the T_{10}, W_{10} and combination of T_{10} and W_{10}

A significant exponential correlation was observed between R_s and T_{10} for the five forest covers ($p < 0.05$). The highest R^2 was observed in S_1 (0.716), but it did not exceed 0.6 in

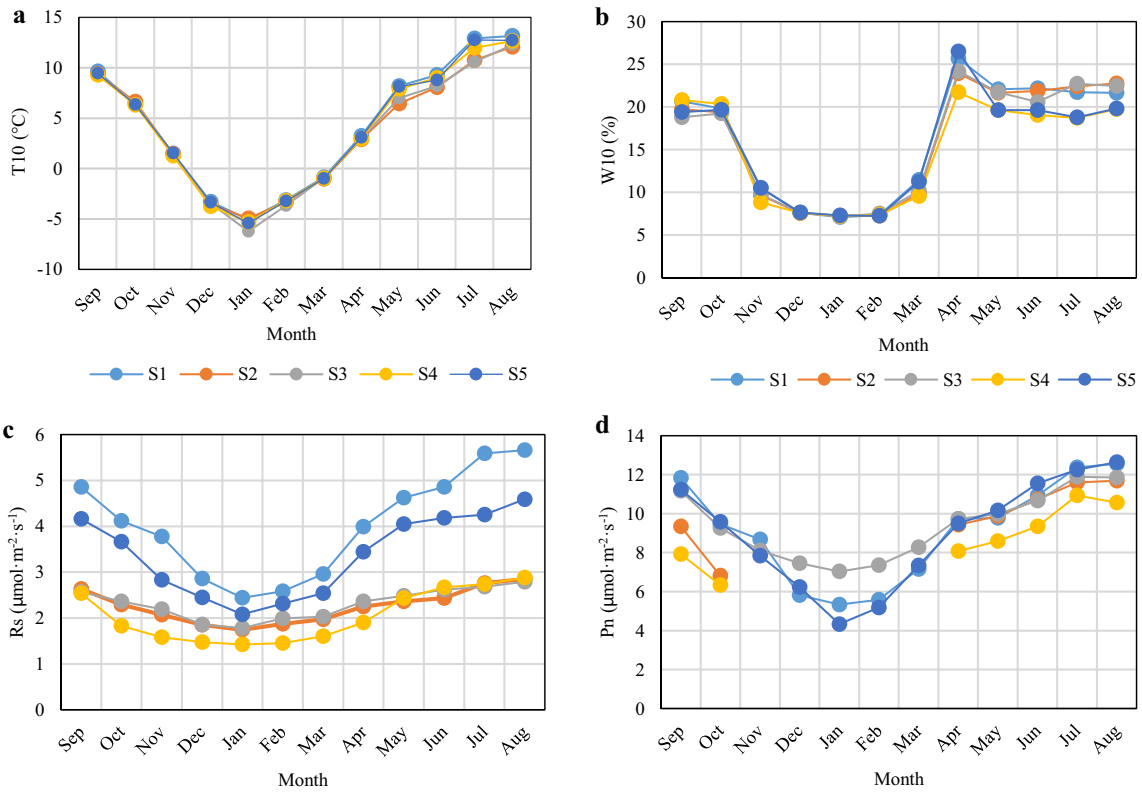


Fig. 3 Monthly variations in soil temperature (T_{10}) and (C) soil moisture content (W_{10}) at 10 cm depth, soil respiration (R_s), and net photosynthetic rate (P_n) in different forest covers (Secondary forest (S_1), *L. principis-rupprechtii* (S_2), *P. crassifolia* (S_3), *P. cathayana* (S_4), and *B. platyphylla* (S_5) plantations) from September 2018 to August 2019. Vertical bars represented the means ± SE

the three other areas (Fig. 4). Q_{10} was highest in S_1 and lowest in S_2. The Q_{10} value of broad-leaf forest was remarkably higher than that of coniferous forest (Table 3).

The goodness of fit for W_{10} was weaker, which was 35% less than the correlation between R_s and T_{10}. Furthermore, the fitted R_s model revealed remarkable effects of W_{10} on forest stands.

For the two-factor model with respect to T_{10} and W_{10}, R^2 was improved to different degrees in all forest covers, which explained 51.8% – 76.1% of the temporal variation in R_s.

Response of R_s to other ecological factors

R_s had a positive correlation with all ecological factors (Fig. 5). However, significant correlations were not observed between R_s and the SOC, TK and soil C:N ratio ($p > 0.05$). The correlation between R_s and P_n is shown in Fig. 6. Research has found that R_s increases with increasing P_n in various forest stands. Moreover, the slope of the relationship was greater for measurements for S_1 and S_5, while the lowest was revealed for S_2. Additionally, R^2 value was lowest in S_4 and highest in S_1.

The relationship between R_s and the combination of T_{10}, W_{10} and P_n

T_{10}, W_{10}, P_n had significant effects on R_s (Figs. 4–6), and photosynthesis can provide the main supply of soil organic substrate for R_s. P_n was an important part of the assessment of R_s via the principal component analysis (mean variance contribution rate was 14.2%, not shown); thus, it was necessary to explore the combined effects of the three factors on R_s. Based on the model between R_s and the combination of T_{10} and W_{10} validated by predecessors, we further introduced P_n as a variable to establish the equation as follows: $R_s = ae^{bT}W^cP_n{}^d$, where a, b, c and d are undermined parameters. The model (Table 4) shows that the model fitting effect improved by introducing the P_n value was compared to the

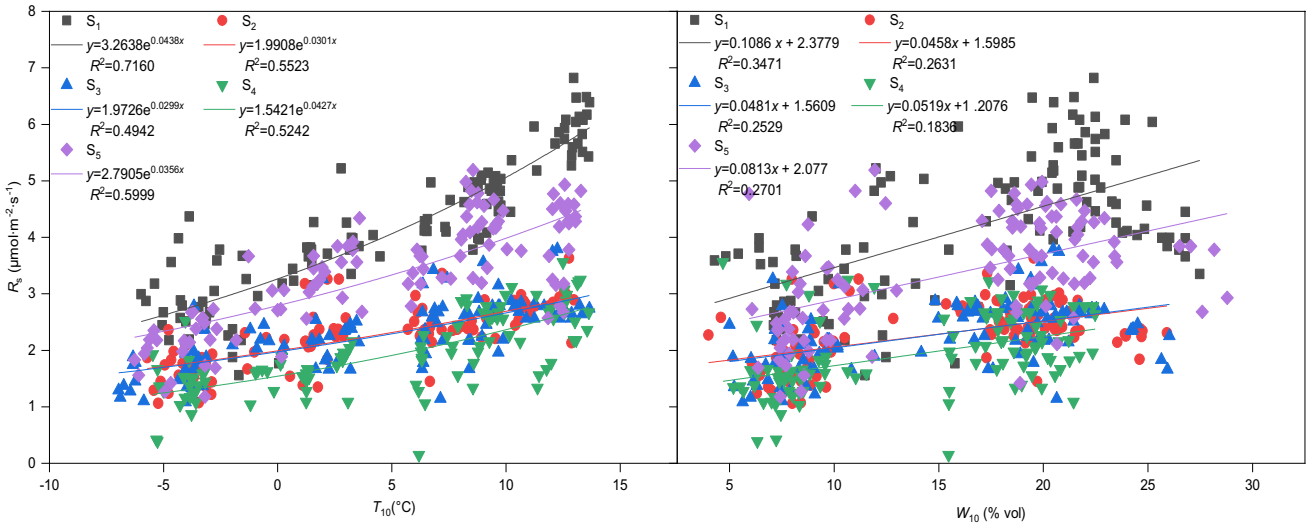
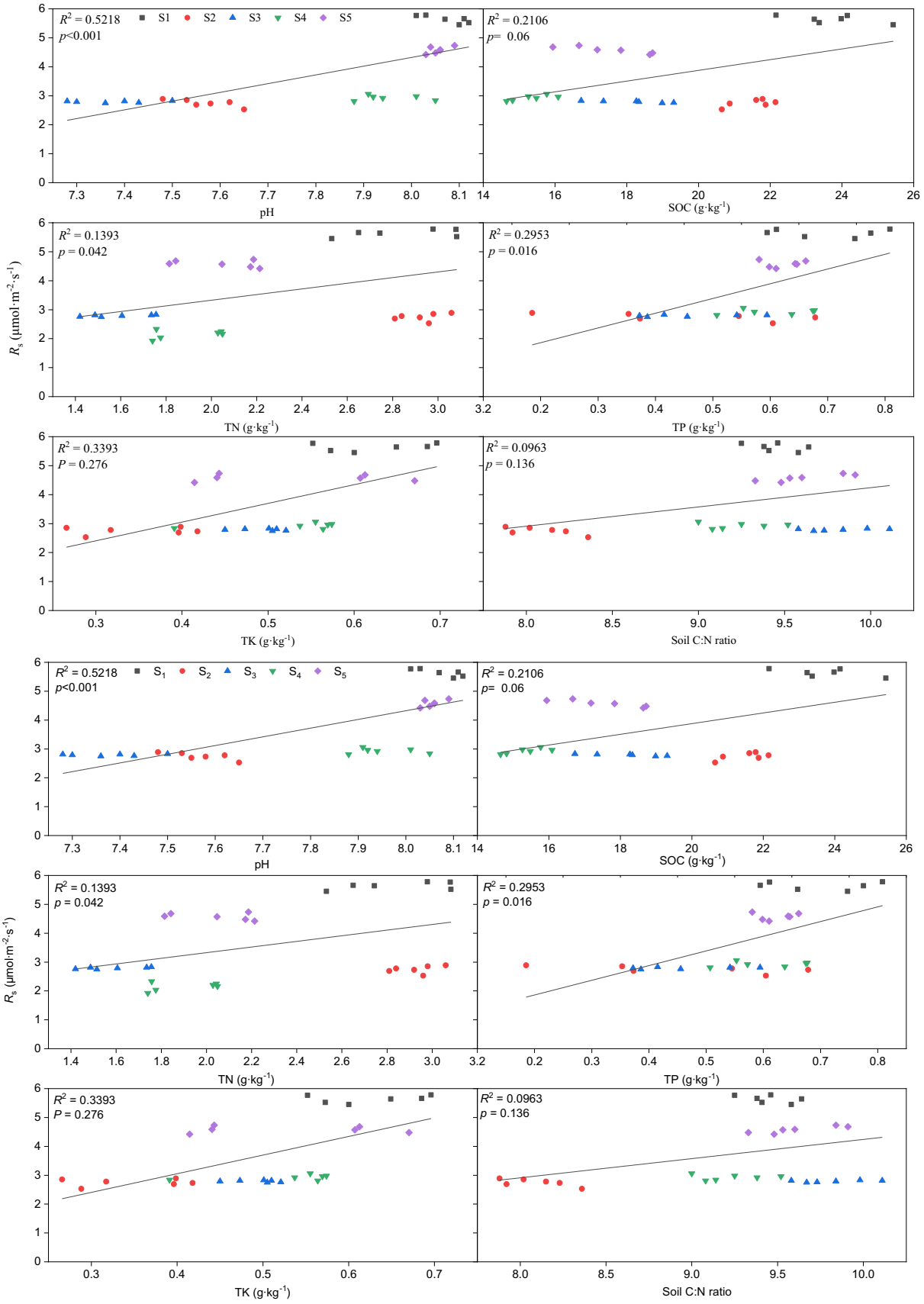


Fig. 4 Exponential and linear fitting relationship between R_s and T_{10} and W_{10}, respectively. R^2 represents the goodness of model fit after adjustment, the same as below. S_1, $S_2 - S_5$ refer to five representative forest covers containing secondary forest (S_1), *L. principis-rupprechtii* (S_2), *P. crassifolia* (S_3), *P. cathayana* (S_4) and *B. platyphylla* (S_5) plantations

Table 3 Regression model parameters of R_s and T_{10}, W_{10} and Q_{10}

Forest covers	$R_s = ae^{bT}$			$R_s = aW + b$			$R_s = ae^{bT}W^c$				Q_{10}
	a	b	R^2	a	b	R^2	a	b	c	R^2	
S_1	3.264	0.0431	0.716**	0.109	2.378	0.347*	4.291	0.051	–0.012	0.761**	1.537a
S_2	1.991	0.0298	0.553*	0.046	1.599	0.263*	1.889	0.032	0.011	0.557*	1.349c
S_3	1.973	0.0300	0.494*	0.048	1.561	0.253*	2.022	0.034	–0.023	0.518*	1.352c
S_4	1.542	0.0427	0.424*	0.052	1.201	0.184*	1.685	0.046	–0.057	0.551*	1.535a
S_5	2.791	0.0352	0.600**	0.081	2.077	0.270*	2.292	0.038	0.059	0.632*	1.419b

Notes Significant correlations at $*p < 0.05$ and $**p < 0.01$, respectively. S_1, $S_2 - S_5$ refer to five representative forest covers containing secondary forest (S_1), *L. principis-rupprechtii* (S_2), *P. crassifolia* (S_3), *P. cathayana* (S_4) and *B. platyphylla* (S_5) plantations


R^2 = 0.5218
p<0.001
S1 S2 S3 S4 S5
pH
R^2 = 0.2106
p= 0.06
SOC (g·kg^{-1})
R^2 = 0.1393
p = 0.042
TN (g·kg^{-1})
R^2 = 0.2953
p = 0.016
TP (g·kg^{-1})
R^2 = 0.3393
P = 0.276
TK (g·kg^{-1})
R^2 = 0.0963
p = 0.136
Soil C:N ratio
R_s (μmol·m^{-2}·s^{-1})
R^2 = 0.5218
p<0.001
S$_1$ S$_2$ S$_3$ S$_4$ S$_5$
pH
R^2 = 0.2106
p= 0.06
SOC (g·kg^{-1})
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P = 0.276
TK (g·kg^{-1})
R^2 = 0.0963
p = 0.136
Soil C:N ratio

◂**Fig. 5** Linear relationship fitted between R_s and pH, SOC, TN, TP, TK and soil C:N ratio for all the forest covers ($N=2$ measurements, a total of 6 replicates). All soil chemical indexes were assessed after the last R_s measurement date.3.5 Fitting relationship between R_s and P_n

relationship between R_s and combination of the T_{10} and W_{10} (Table 3).

Discussion

T_s and soil water content (SWC) are the main environmental factors controlling R_s, and their changes will affect R_s in different stand types to different degrees. Limited diurnal variations occurred T_{10} and W_{10} in different forest covers because of the influence of closed canopies, and the result was different from the fluctuation of R_s, indicating that soil physical factors are not the main drivers of R_s dynamics at the diel scale. These phenomena were in line with findings in arid and semiarid regions(Jia et al. 2018). Furthermore, the R_s of the broad-leaved species was much higher than that of coniferous species during spring, summer, and autumn, which may be due to the increased alduronic acid secreted by the leaves of S_2 and S_3, which caused soil acidification (refer to the pH value in Table 1) and slow decomposition of litter, thereby inhibiting the activity of microorganisms to reduce heterotrophic respiration. The R_s values in the daytime (photosynthesis was carried out synchronously) were greater than those at night, indicating that photosynthesis was coupled with respiratory mechanisms on a daily time scale. The seasonal variation trend of R_s was conspicuously regulated by T_{10} and W_{10}, in accordance with Chen's research on different subalpine ecosystems (Chen et al. 2014), and demonstrated the higher sensitivity of R_s to T_{10} and W_{10} on a seasonal scale compared to that on the daily scale. Moreover, photosynthetic productivity was an important driver of soil CO_2 flux, not only on the daily time scale, but also on the seasonal and annual scales (Michael et al. 2008). In our study, the monthly variations in R_s and P_n maintained a high degree of consistency in different forest covers. Even in the winter when S_2 and S_4 lacked photosynthetic products, their R_s values simultaneously decreased to the minimum values. Our research also found that the R_s of S_1 was significantly higher than that of pure forests throughout the year. By comparing the soil characteristics of each forest (Table 1), we found that the soil bulk density and the SOC, TN, TP and TK were significantly lower and higher than those of other forests, respectively. This result showed that the secondary forest structure (multilayer forest) was the most reasonable and could effectively alleviate intraspecies competition and promote plant growth and metabolism, thereby providing material conditions for carbon cycling.

T_s contributes to regulating R_s by its effects on plant root growth, microbial activity, and litter decomposition; therefore, an exponential regression model was established for both (Song et al. 2013). Based on previous studies, we adjusted the parameters of the model to apply to the study area, then established a significant exponential model to demonstrate the regulatory effect of T_{10} on R_s, thereby providing theoretical support for the prediction of CO_2 flux variations in alpine hilly areas under global warming. The correlation coefficient between R_s and T_{10} ranged from 49.4% in S_3 to 71.6% in S_1. The reason for the difference may be due to the dissimilarity of the root systems and microbial activity (Chen et al. 2010), and even the regulation of photosynthesis by T_s ($R^2=0.73$, $p<0.05$) in plants may affect R_s. The correlation model of R_s and T can explain most of the seasonal and diel changes in soil C emissions, although the effect is not identical. Other factors such as soil moisture content affect R_s for a certain period of time. Therefore, we established a linear regression model of R_s and W_{10}. The correlation between R_s and SWC was significantly different in five forest types, which might be because the variation in W_{10} affected the input of carbon and the decomposition of litter and soil organic matter, thus indirectly affecting heterotrophic respiration and carbon output (Moyano et al. 2013). The correlation coefficients of the model were significantly lower than those based on R_s and T_{10}, which may have been caused by factors such as rainfall and severe evapotranspiration, and the related models established by SWC were not stable enough, as shown by the CV values (Fig. 3) for the forest types. In addition, sufficient precipitation occurred during study period, indicating that SWC was not a limiting factor for R_s.

Wang et al. (2006) believed that T_s is a great indicator for estimating R_s in a specific ecosystem, and verified the Q_{10} function to estimate the reliability of R_s, which is also confirmed by most ecosystems. The response of soil CO_2 emission to T_s can be described by Q_{10} which is the T_s coefficient of the reaction (Ma et al. 2019). In this study, the Q_{10} value of broad-leaf forest was remarkably higher than that of coniferous forest, which was not in line with Zheng (Zheng et al. 2009), who found that the Q_{10} in deciduous forests was significantly higher than that in evergreen forests, and the Q_{10} in coniferous forests was significantly higher than that in evergreen broad-leaf forests. This difference may be because Q_{10} is not a long-term reflection of temperature sensitivity, but rather a comprehensive response to temperature fluctuations, root biomass and activity, humidity conditions, and other unknown variables (Janssens and Pilegaard 2003), thus resulting in indistinctness. Scholars have proposed that W_{10} thresholds exist in different forests. When W_{10} is higher than the threshold, the response of R_s to T_{10} may be confined by limiting aeration and CO_2 diffusion, and

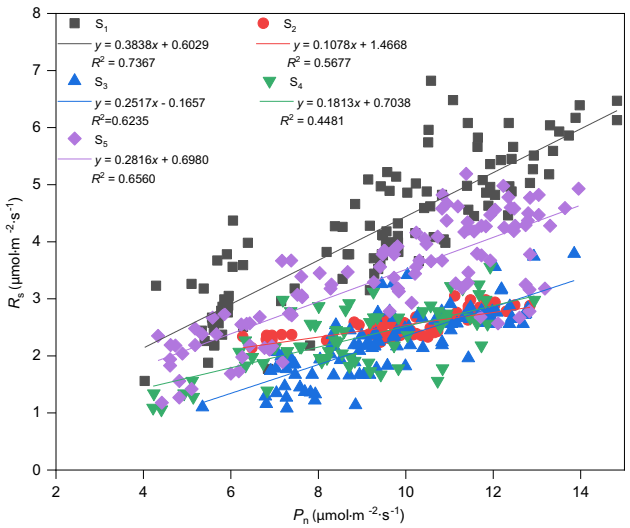

Fig. 6 Linear fit of relationship between R_s and P_n, which is maintained at the same level of T_{10} and W_{10}. S_1, S_2-S_5 refer to five representative forest covers containing secondary forest (S_1), *L. principis-rupprechtii* (S_2), *P. crassifolia* (S_3), *P. cathayana* (S_4) and *B. platyphylla* (S_5) plantations

the decrease in soil microbial activity in a low oxygen environment may also lead to the reduction of soil CO_2 emissions, thereby restraining the sensitivity of R_s to T_{10} (Xu and Qi 2001b; Rey et al. 2002; Chen et al. 2010). Although T_{10} was not significantly different between the different forest stands, other ecological biological factors were significantly different, including SOC, TN, TP, TK, pH, soil bulk density and P_n. Moreover, Q_{10} was highest in S_1 because it belonged to the enclosed forest protected from human activities, and S_1 was characterized by a sufficient supply of soil organic substrate, higher root biomass, and microbial activity, and more complex and stable species composition compared to other forests. However, this result also implied that the carbon cycle might experience a greater disturbance under global warming. Therefore, the process of global warming and carbon cycle promote and influence each other and are complementary.

The combination of T_s and SWC on R_s is critical to understanding the mechanisms of climate control on R_s and its components (Ma et al. 2019). The response of R_s to T_{10} and W_{10} in this study area has been proven, and it is worth exploring whether there is an interactive or complementary effect of T_{10} and W_{10} on R_s. We established a two-factor model combining W_{10} and T_{10} compared to the model-based only on T_{10} or W_{10}, which improved R^2 to different degrees, this circumstance has been ascertained by others research (Zhang et al. 2010; Gao et al. 2018; Ma et al. 2019). According to our results, the variation trend of R_s increased with the escalation of W_{10} and T_{10}. From May to August, when W_{10} remained basically stable, the increase in T_{10} promoted the increase in R_s by boosting the root system and microbial activity.

When exploring the response of R_s to other ecological environmental factors, we observed that the variation in R_s was not in conformity with that of SOC, TK and the soil C:N ratio, which was also confirmed by Gao et al. (2018) in a study of the correlation between R_s and environmental factors. In addition, R_s was weakly consistently correlated with TN and TP (Nielsen and Becky 2015; Wertin et al. 2018). The findings indicated that the combined indicators rather than a single factor regulate the changes of R_s, which complicates the evaluation of R_s (Okin et al. 2016). Soil properties can be influenced by forest types and act on soil microbial and root activity (Lu et al. 2014). Our research found that R_s can be significantly affected by pH, which is further evidence that coniferous forest leaves contribute to soil acidification, thus reducing R_s.

Previous research revealed that T_{10} and W_{10} together could explain more than 75% of the variation in R_s (Keith et al. 1997). Since the components that affect changes in R_s are not completely clear, we are particularly interested in the contribution of P_n to R_s with species of contrasting functional types. We analyzed the correlation between the P_n value and R_s of each forest cover type and found that P_n was significantly positively correlated with R_s, which is consistent with studies showing the close coupling of *A. hymenoides* and *A. confertifolia* leaf-level P_n and R_s (Wertin

Table 4 The regression model parameters for $R_s = ae^{bT}W^cP_n{}^d$. The equation is established according to the synchronous measurement data of each index

Forest cover	Regression model parameters values					
	a	*b*	*c*	*d*	R^2	*p*
S_1	2.0458	0.0331	–0.1192	0.3811	0.7860	0.0222
S_2	1.4052	0.0132	–0.0282	0.2511	0.6221	0.0037
S_3	0.1702	–1.8370	0.0101	1.1232	0.6305	0.0292
S_4	0.8291	0.0131	–0.1547	0.6122	0.5710	0.0324
S_5	0.9394	–0.6248	–0.0010	0.8973	0.6971	0.0325

Notes S_1, S_2-S_5 refer to five representative forest covers containing secondary forest (S_1), *L. principis-rupprechtii* (S_2), *P. crassifolia* (S_3), *P. cathayana* (S_4) and *B. platyphylla* (S_5) plantations**.** (*b* is the parameter that needs to be corrected in the formula; *T* is the temperature)

et al. 2017, 2018). Other studies have demonstrated the close correlation between P_n and R_s in dryland ecosystems (Chen et al. 2009). This result showed that the photosynthetic C supply acted as a driving factor for R_s and P_n, and regulated R_s by stimulating root respiration and heterotrophic respiration of root deposition. Moreover, studies have also suggested a more compact coupling between photosynthetic products and R_s than between R_s and other factors (Vargas et al.; 2010a, b; Jia et al. 2018). We can also support this result by analyzing the correlation between the P_n of a single-leaf horizontal and R_s; R^2 was higher than that of the model based only on W_{10} and T_{10}. Furthermore, the R^2 between P_n and R_s was lowest in S_4 and highest in S_1. We speculated that S_1 was located in the fenced-in zone, which was not disturbed by human activity, and that production and behaviors would introduce more substrate and change the mechanisms underlying underground C supply, thereby reducing the effect of photosynthesis on R_s. But why is the correlation coefficient lowest in S_4 if it is an artificial forest subjected to more human disturbance? The daily change in P_n is bimodal with solar radiation, temperature, and humidity in most of the observation periods, and the severe water consumption characteristics of *P. cathayana* reduced the biomass and microbial activity of the forest. In addition, the high incidence of black spot disease in August severely inhibited leaf photosynthesis during period of growth and metabolism, as shown in Fig. 3. Therefore, to more comprehensively evaluate the main factors controlling R_s in different forest ecosystems in subalpine hilly areas, we introduced P_n to establish a three-factor model. The results exhibited a significant improvement in the fitting correlation coefficient compared to that of the two-factor model based on the combination of T_{10} and W_{10}. Our results suggest that the control of R_s by the environment (moisture and temperature) and photosynthesis may be spatially and temporally homeostatic in the region; thus, the model was feasible for describing the dynamic variation in the R_s and the carbon cycle under different forest covers.

However, the pattern of underground C supply and distribution is not yet clear. Although these findings help fill some gaps in knowledge of R_s dynamics in different forest ecosystems under current climatic conditions, further research should focuse on the driving factors of autotrophic respiration and heterotrophic respiration, and the response of microorganisms to climate change needs to be explored.

Conclusion

During spring, summer, and autumn, the diurnal variations in R_s were significantly greater in the afternoon than at other times, and the R_s was pronouncedly higher for broad-leaved species than for coniferous species in the five typical forest covers. Our study also found that R_s could be significantly affected by soil pH, which provided further evidence that coniferous forest leaves contribute to soil acidification, thus reducing R_s. Furthermore, soil physical factors are not the main drivers of R_s dynamics at the diel scale; however, the trend in the monthly variation trend of R_s was consistent with that of T_{10} and P_n. The R_s of S_1 was significantly higher than the value found in pure forests throughout the year.

The R^2 for the model based on R_s and T_{10} was significantly higher than for the model based on R_s and W_{10}. Moreover, the two-factor model that combined T_{10} and W_{10} with adjusted parameters improved the R^2 value at a different level compared with the model based only on T_{10} and W_{10}, indicating that the R_s was influenced by the combined effect of T_{10} and W_{10}, which was interactive or complementary in different forest ecosystems in the alpine hilly region. The Q_{10} value for the broad-leaved forest was remarkably higher than for the coniferous forest, and the highest value was discovered in the secondary forest. Our findings showed that a combination of soil chemical properties rather than a single factor may regulate the changes of R_s, which complicates the evaluation of R_s.

By evaluating the correlation between the P_n at the single-leaf level and R_s, we proved that P_n was closely coupled with R_s in all the measured forests. Furthermore, the R^2 between P_n and R_s was lowest in *Populus cathayana* plantations and highest in the secondary forest. The results showed that the three-factor model presented significant improvements in R^2 compared to the two-factor model based on the combination of T_{10} and W_{10} and thus is, feasible for describing the dynamic variation in R_s.

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