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The effect of postfire regeneration pattern on soil respiration in the boreal forest of China



Lixue Yang¹, Chengfeng Shan¹, Siyu Zhou¹, Yuchun Yang², Huifeng Liu³ and Fangyuan Shen^{1*}

Abstract

Background As the second largest carbon flux between the atmosphere and terrestrial ecosystems, soil respiration involves multiple components of ecosystem production. Revealing soil respiration in forests with different postfire regeneration patterns is critical for determining appropriate restoration strategies in response to increasing wildfire disturbances. Here, we examined the influence of five postfire regeneration patterns (L: *Larix gmelinii* monocultures, LB: *L. gmelinii* and *Betula platyphylla* mixed plantations, P: *Pinus sylvestris* var. *mongolica* monocultures, PB: *P. sylvestris* var. *mongolica* and *B. platyphylla* mixed plantations, N: naturally regenerated forests) on soil heterotrophic respiration (Rh) and total respiration (Rs).

Methods Trenching was implemented to monitor soil heterotrophic respiration. We used partial least squares path modeling methods to estimate the different environmental factors regulating soil respiration across forest types.

Results The results showed that forest type and season had significant effects on Rs and Rh. Rh was the dominant part of Rs for all forest types (68.84 ~ 90.20%). Compared to naturally regenerated forests, Rs and Rh under L, LB, and PB had higher rates (P < 0.05), while Rs and Rh under P had lower rates (P < 0.05). The temperature sensitivities of Rs under different forest types were 2.316 (L), 1.840 (LB), 1.716 (P), 1.665 (PB), and 2.096 (N).

Conclusions Forests regenerated with artificial participation established their plant communities visibly faster than naturally regenerated forests. Mixed species plantation regeneration demonstrated an improvement in soil respiration compared to naturally regenerated forests but had a lower temperature sensitivity of soil respiration than their respective monocultures. Soil temperature and moisture dominated the influence factors on soil respiration throughout the broader seasonal shifts. However, for a single season, forest productivity and soil properties have a greater impact on soil respiration. This study extends our knowledge of the interaction mechanism between soil respiration and environmental variables in boreal forests and contributes to improving confidence in global carbon cycling model predictions.

Keywords Soil respiration, Boreal forest, Postfire regeneration, Litter, Soil property

Resumen

Antecedentes Como segundo flujo de carbono más grande entre la atmósfera y los ecosistemas terrestres, la respiración del suelo implica múltiples componentes en la producción de un ecosistema. El dilucidar la respiración de los suelos en bosques forestales con diferentes patrones de regeneración post fuego es crítica para determinar estrategias de restauración apropiadas en respuesta al aumento del disturbio fuego. Examinamos aquí la influencia de cinco patrones (o tipos forestales) de regeneración post fuego (L: monocultivos de *Larix gmelinii*, LB: L. plantaciones

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mixtas de *gmelinii* y *Betula platyphylla*, P: monoculturas de *Pinus sylvestris* var. Mongólica, PB: plantaciones mixtas de *P. sylvestris* var. mongolica y *B. platyphylla*, y N: bosques regenerados naturalmente), en la respiración heterotrófica del suelo (Rh) y respiración total (Rs).

Métodos La respiración heterotrófica del suelo se monitoreó en hoyos o trincheras cavadas en el suelo en cada patrón de regeneración. Usamos como método el paso de modelos de mínimos cuadrados parciales para estimar los diferentes factores ambientales que regulan la respiración del suelo entre los diferentes tipos forestales.

Resultados Los resultados muestran que los tipos forestales y la estación del año tienen efectos significativos en Rs y Rh. La respiración heterotrófica (Rh) fue la porción dominante del Rs para todos los tipos forestales (68.84~90.20%). Comparado con bosques regenerados naturalmente, Rs y Rh, bajo tipos L, LB, y PB tienen tasas más altas (P < 0.05), mientras que Rs y Rh bajo el tipo forestal P tiene tasas más bajas (P < 0.05). La sensibilidad de la temperatura de Rs bajo los diferentes tipos forestales fue de 2,316 (L), 1,849 (LB), 1,716 (P), 1,665 (PB) y 2,096(N).

Conclusiones Los bosques regenerados de manera artificial establecieron sus comunidades vegetales visiblemente más rápidamente que los bosques regenerados naturalmente. La regeneración de plantaciones mixtas demostró una mejora en la respiración del suelo comparada con la regeneración natural, pero tuvieron una sensibilidad de la temperatura de la respiración del suelo más baja que sus respectivas monoculturas. La temperatura y humedad del suelo dominaron los factores que influencian la respiración del suelo a través de las amplias variaciones estacionales. Sin embargo, para una sola estación, la productividad y propiedades del suelo tuvieron los impactos más grandes en la respiración del suelo. Este estudio extiende nuestro conocimiento sobre los mecanismos de interacción y contribuye a mejorar la confianza sobre las predicciones de los modelos sobre el ciclo del carbono a nivel global.

Background

As the second largest carbon flux between the atmosphere and terrestrial ecosystems (Lei et al. 2021; Xu et al. 2015), soil respiration is a vital process in global carbon cycling. Soil stores a much greater share of organic carbon than the vegetation in boreal forests (Laganière et al. 2012; Lal 2005). The boreal forest is the world's largest land biome, accounting for more than 30% of the total terrestrial pool of living biomass and 20% of the global organic carbon (Akande et al. 2023; DeAngelis 2008), making the soil carbon balance the cornerstone of climate change mitigation (Mack et al. 2021). However, soil respiration response to different regeneration strategies after fire is poorly understood. Large areas in boreal forests are disturbed by wildfires every year (Ohlson et al. 2009), and the fire frequency in boreal forests is expected to increase with future climate change (Bond-Lamberty et al. 2007). This trend may result in a shift of boreal forests from a carbon sink to a net carbon contributor (DeAngelis 2008), making the restoration of forest cover a fundamental action in mitigating climate change.

Revealing the characteristics of soil respiration at plot or ecosystem levels helps us better understand the characteristics of carbon dynamics at regional or global levels. Soil respiration can coarsely be partitioned into autotrophic and heterotrophic components, both of which are carried out continuously in every cell of all living organisms in the soil. As a consequence, soil respiration involves a range of biological, chemical, and physical processes at each of the hierarchical levels from cell to planet, which can be regulated by multiple environmental variables such as, soil temperature (Laganière et al. 2012; Luo and Zhou 2006a), moisture (Maier and Kress 2000), substrate supply (Liu et al. 2021b), soil texture (Singh et al. 2023), nitrogen content (Peng et al. 2020; Xing et al. 2022), and soil pH (Li et al. 2020; Xu and Qi 2001).

Considering that temperature exerts a dominant influence on all aspects of respiration processes, the sensitivity of soil respiratory processes to temperature, known as the Q_{10} factor, is a principal parameter for benchmarking the intensity of carbon flux feedback between soil and climate (Li et al. 2020). This parameter has garnered widespread attention (Haaf et al. 2021; Mahecha et al. 2010; Qin et al. n.d.). However, on a regional scale, the aboveground plant community may play a crucial role in mediating soil respiration (Luo et al. 2011; Xu et al. 2015) by controlling a series of biotic and abiotic factors (Lei et al. 2021). For example, changes in species composition within different forest types could alter the quantity and quality of organic matter input into the soil by their contrasting phenological characteristics including photosynthesis (Wan and Luo 2003), root systems (Boone et al. 1998), and litter production and decomposition (Peng et al. 2020), which might further affect soil respiration through the substrate supply pathway (Metcalfe et al. 2011; Xu et al. 2015).

The influences of wildfire on soil respiration were linked to the degree of fire severity (Zhou et al. 2023). Gui et al. (2023) identified the impacts of fire severity (high, moderate, and low severity) on soil respiration based on a meta-analysis including 91 studies on fires across 116 global sites. The fires of both high and low severity have subdued the soil respiration, potentially as a result of the diminished soil microbial biomass following the fires (Dooley and Treseder 2012). However, moderate severity fires exert a negligible impact on soil respiration, likely because the positive effects of charcoal formation during such fires offsets the negative effects of soil C pool depletion, resulting in a neutral response of soil respiration to the fire (Gui et al. 2023).

The postfire regeneration strategy may be a key factor influencing this grim trend, as a recent study showed that carbon loss from wildfires in boreal forests could be offset by the increased dominance of deciduous trees in postfire regeneration (Mack et al. 2021). Soil respiration has a significant effect on altering the net ecosystem carbon balance since small changes in soil respiration rates would have a major influence on annual increases in the concentration of atmospheric CO_2 (Gomez-Casanovas et al. 2012). Different forest regeneration patterns after fire are usually accompanied by disparate soil respiration modes given their diverse trajectories of soil and plant community successions (Buotte et al. 2019; Cruz-Alonso et al. 2019).

Despite the importance of soil respiration in ecosystem carbon budgets, incomplete knowledge of the underlying mechanism of biophysical factors controlling soil respiration after fire still limits our capacity for predicting the feedback of forest regeneration patterns to soil respiration. The Black Dragon Fire of 1987 in China was one of the most devastating wildfires on Earth in the past several hundred years (Fang et al. 2021), which burned more than 1.30 million hectares of wildland and forests, with severely burned areas accounting for 52% (Xu et al. 2020), leading to the extensive loss of the forest canopy and associated timber resources. Natural and intentional regeneration of tree cover was used for reforestation after the fire on the high-severity patches in the following year. Thirty-four years after establishment of postfire forest recovery project, we investigated the implications of five typical regeneration patterns involving three strategies and two dominant tree species. The two dominant tree species were Larix gmelinii and Pinus sylvestris var. mongolica. The three strategies included monoculture, mixed species plantation, and naturally regenerated. Monoculture plantations dominate existing commitments to restore forest cover globally (Bukoski et al. 2022). The establishment of mixed plantations is a promising way to address productivity declines in long-term monocultures. In this study, mixed plantations were established at a ratio of 7 to 3 for artificial and naturally regeneration. Naturally regenerated forests usually occupy the largest regeneration area after a wildfire around the world.

In 2022, we monitored soil respiration in forests regenerated with five patterns to (1) compare the effects of different forest types on soil respiration and (2) identify the key moderators, such as forest productivity and soil conditions, that regulate soil respiration in postfire forest ecosystems. We hypothesized that (1) artificial regeneration forests can increase soil respiration compared to naturally regenerated forests, considering that the artificial forests usually exhibit a higher level of forest productivity. (2) Soil temperature and moisture are the primary factors affecting soil respiration in terms of overall seasonal changes.

Methods

Study area and design

Study sites were selected in the Xiufeng Forest Farm (51° 24′ N~52° 44′ N, 124° 12′ E~125° 14′ E) of Tahe County, northern Greater Khingan Mountain range, China. This area has a cold temperate climate. In the last 50 years, the mean annual temperature has been -2.2°C, with the average lowest temperature of -45.8 °C occurring in January. The mean annual frost-free period is 98 days, with a mean annual precipitation of 473.8 mm (Tahe County climatological survey, Heilongjiang, China). Precipitation is mainly concentrated in the growing season. The zonal soil is Podzol (mainly brown coniferous forest soil) with acidic pH. The parent material of the soil is primarily composed of the residual and colluvial of granite and volcanic rocks. The average elevation is 357 m above sea level. The secondary forest is characterized by a low diversity of tree species, which is dominated by gymnosperms, including Dahurian larch (L. gmelinii) and Mongolian pine (P. sylvestris var. mongolica), and accompanied by varying proportions of angiosperms such as white birch (Betula platyphylla) and David poplar (Populus davidiana). Dahurian larch covers more than 70% of the boreal forest ecosystems in northeastern China (Jiang et al. 2002).

In the spring of 1988, two monoculture types (L: *L. gmelinii* monocultures, P: *P. sylvestris* var. *mongolica* monocultures) were established with 2-year-old seed-lings. The interrow and intrarow space distances were designed to be 2 m×1.5 m. The monocultures were tended twice a year for the next 3 years, including the removal of naturally regenerated birch. The establishment of mixed plantation types (LB: *L. gmelinii* and *B. platyphylla* mixed plantations, PB: *P. sylvestris* var. *mongolica* and *B. platyphylla* mixed plantations) was performed by the alternate mixing of two "belts". "Belt A" was 7 m wide and consisted of seven rows of *L. gmelinii* or *P. sylvestris* var. *mongolica*, while "Belt B" was 3 m wide and regenerated naturally. The "Belt A" in mixed plantations had the same afforestation specifications as

monocultures. However, the naturally regenerated birch was preserved in the forest tending operations.

All study sites originated from the same wildfire that occurred in May 1987, and all stands were regenerated after clear-cutting of overfire wood on the highseverity patches. Two monoculture types and two mixed plantation types served as treatments, while naturally regenerated forests were selected as controls. Three representative sites with a similar slope $(11 \sim 13^\circ)$ were randomly selected to minimize the spatial heterogeneity of soil respiration (Table S1). In each study site, another three groups of repeated standard plots $(20 \times 30 \text{ m})$ were also randomly established. Within each plot, we investigated the tree species, tree height, and diameter at breast height (DBH) for all trees. The tree heights were measured using an ultrasonic altimeter (Vertex IV, Haglöf, Sweden). The tree's diameter was measured at a height of 1.30 m above the ground, employing a diameter tape. The basal area of each tree was determined using the formula: basal area = $\pi \times (DBH/2)^2$. The stand volume of each tree was calculated according to the local standard volume model in the tree volume tables of China (Liu 2017).

Soil respiration measurements

Soil respiration determination was manually implemented seasonally (May, July, and September) by using an LI-COR 8100 soil CO₂ flux system (LI-COR. Inc., Lincoln, NE, USA). We quantified the soil heterotrophic respiration based on the trenching method (Luo and Zhou 2006b). We set up a 2×2 m subplot in each plot and dug trenches to a depth of 50 cm (20 cm below the rooting depth) around the subplot (Fig. S1A-D). The trenches were backfilled after lining with double layers of polyethylene sheet to prevent root ingrowth (Fig. S1E). Living plants inside each subplot were clipped at the soil surface, and the clipped plant materials were left in the subplots (Fig. S1F). All the subplots were completed in September 2021. Six polyvinyl chloride (PVC) collars (20 cm in diameter \times 7 cm in height) were inserted 5 cm into the soil within each plot at the beginning of the experiment. Three PVC collars were inserted randomly in the trenched subplot, and three PVC collars were inserted outside the trenched subplots. The observed CO₂ efflux in the subplots (trenched) was considered the soil heterotrophic respiration rate (Rh), and the CO₂ efflux measured outside the subplots was regarded as the soil total respiration rate (Rs).

The Rs and Rh measurements were completed between 9:00 AM and 11:00 AM on the last 10 days of May, July, and September 2022. During the Rs and Rh measurement process, soil temperature (ST) and moisture (SM, volumetric water content, % v/v) at a depth of 5 cm (Hu et al. 2021) were recorded by a temperature probe (p/n

8100–201) and a soil moisture probe (ECH20 EC-5; p/n 8100–202), respectively. We avoided taking measurements on rainy days and within 24 h after rainfall events. In addition, the diurnal variation in Rs was also measured for each treatment to assess the difference in CO_2 effluxes between midmorning (9:00 ~ 11:00 AM) and the average of 24 h. We kept the PVC collars free of living plants to eliminate aboveground plant respiration during all measurements of soil respiration.

Soil and litter sampling and analyses

After removing the litter layer, soil cores of 15 cm depth were collected by the five-point sampling method by utilizing a soil auger (5 cm diameter) in each plot. Soil cores from the same plot were mixed into a composite sample. The fresh soil samples were sieved through a 2-mm sterilized sieve to remove visible roots, rocks, and other residues. A part of the subsamples was air-dried for physicochemical analysis. Another set of subsamples was stored at 4 °C for soil available nitrogen content determination.

The cutting ring method was used to determine soil bulk density (BD) and total porosity (STP). Soil texture analysis was conducted using air dried soil samples. After being sieved through a 2-mm sieve, these samples were made into a suspension. A 6% H₂O₂ solution was used to remove organic matter from the soil samples through the process of heating. 0.5 mol/L NaOH was used as a dispersing agent, to which distilled water was added to achieve a final volume of 250 ml. The solution was then heated to boiling and maintained at this temperature for 1 h. Particles within the size range of 2 to 0.25 mm were separated using a 0.25-mm sieve. Soil particles smaller than 0.25 mm were washed into a 1 L sedimentation cylinder using the pipette method, which is based on Stokes' law. The percentage content of each particle size fraction was calculated based on their respective masses. The soil texture was classified according to the USDA's texture triangle (Table S2).

The soil total carbon (TC) and total nitrogen (TN) contents were analyzed after tableting using a J200 Tandem laser spectroscopic element analyzer (Applied Spectra, Inc., Fremont, CA, USA). Soil organic carbon (SOC) was determined by dichromate oxidation. A continuous flow analytical system (AA3, Seal Co., Germany) was used to measure the contents of soil ammonium (NH₄) and nitrate nitrogen (NO₃).

We determined the litter yield and decomposition rate for each forest type. Litter collection was performed by randomly setting three 1×1 m litter collection devices in each plot during the peak litter fall period of July 31 to October 31, 2021 (Fig. S2A). The litter collected in September 2021 was oven dried (60 °C) to a constant weight and then placed into 50- μ m mesh nylon decomposing bags with a size of 15×15 cm for decomposition determination. Each nylon bag contained 5 g of litter and was placed on the litter layer of each plot in September 2021 (Fig. S2B, C). Litter bags (10 bags×45 plots=450 bags in total) were retrieved in September 2022 (Fig. S2D). After carefully removing the soil and impurities outside the decomposition bag, the remaining litter materials were taken out and oven dried (60 °C) to a constant weight to calculate the annual decomposition rate.

Statistical analysis

We performed two-way ANOVA to examine the effects of forest type and season on soil physicochemical properties. One-way ANOVA was used to determine the differences in forest stand characteristics among different forest types. Before the post hoc test, we examined the normality of the data and homogeneity of variances by the Kolmogorov – Smirnov test and Levene's test, respectively. We conducted repeated-measures ANOVA to investigate the effect of forest type and season on Rs and Rh, where forest type served as the between-subject factor and season as the within-subject factor. The homogeneity assumption of repeated measures data was assessed with Mauchly's test, and the non-parametric ANOVA test was adopted if the Mauchly's test was violated. The abovementioned statistical analyses were conducted using SPSS 26.0 (SPSS Inc., Chicago, IL, USA).

We finally modeled the relationship between the soil respiration rate (Rs and Rh) and soil temperature through the van't Hoff exponential function (1) (van't Hoff, 1884) after comparing the R^2 values of multiple classical empirical models.

$$R = ae^{bT} \tag{1}$$

$$O_{10} = e^{10b} (2)$$

where *R* is the measured soil respiration rate (μ mol CO₂ m⁻² s⁻¹), and *T* is the soil temperature (°C) at a depth of 5 cm (Xing et al. 2022). The sensitivity of soil respiratory processes to temperature (Q_{10}) was calculated using Eq. 2, where the parameter *b* is obtained by calculating Eq. 1.

A nonlinear regression model was used to establish the relationship between the soil respiration rate (Rs and Rh) and soil moisture. To quantitatively describe the direct and indirect relationships between environmental controlling factors and soil respiration, we established a structural equation model by partial least squares path modeling (PLS-PM). The environmental controlling factors were divided into nine categories, including forest productivity, soil texture, soil bulk density, soil moisture, soil porosity, substrate supply, C:N ratio, soil temperature, and Rs. The statistical analyses were performed by the "plspm" package (Sanchez 2013) in R software v4.2.2 (https://www.r-project.org/).

Results

Forest stand, soil, and litter properties in different forest types

The forest stand characteristics, including tree density, DBH, basal area, tree height, and stand volume, varied among the different forest types (P < 0.001, Table 1). Compared to naturally regenerated forests, mixed plantations (LB and PB) had higher tree densities (P < 0.05), while monocultures (L and P) had lower tree densities (P < 0.05). *L. gmelinii* monocultures had the maximum DBH (9.6 ± 0.4 cm) and tree height (8.05 ± 0.49 m). *P. sylvestris* var. *mongolica* monocultures had the maximum basal area (24.40 ± 1.19 m² ha⁻¹) and stand volume (131.59 ± 4.87 m³ ha⁻¹). Naturally regenerated forests had the minimum DBH (5.3 ± 0.3 cm), basal area (6.03 ± 0.58 m² ha⁻¹), tree height (4.81 ± 0.21 m), and stand volume (33.63 ± 4.24 m³ ha⁻¹) among all forest types.

Table 1 Forest stand characteristics in different forest types

			<i></i>			
Forest types	Canopy cover (%)	Tree density (trees ha ⁻¹)	DBH (cm)	Basal area (m ² ha ⁻¹)	H (m)	Stand volume (m ³ ha ⁻¹)
L	70.8±0.7 ABC	2400±10 C	9.6±0.4 A	20.87±1.64 B	8.05±0.49 A	118.23±11.14 A
LB	74.9±1.3 A	3478±173A	8.1±0.3 B	21.02±0.57 B	7.66±0.16 A	108.73±8.78 AB
Ρ	68.7±1.2 BC	2578±39C	8.9±0.2 AB	24.40±1.19 A	7.74±0.06 A	131.59±4.87 A
PB	72.4±1.5 AB	3222±103 A	8.5 ± 0.2 B	18.27±0.47 B	7.64±0.18 A	91.44±4.40 B
Ν	66.2±1.1 C	2756±120B	5.3±0.3 C	5.99±0.59C	4.81±0.21 B	33.63±4.24 B
One-way ANOVA	F=7.49***	F=41.18***	F=22.49***	F=50.71***	F=38.04***	F=25.47***

Mean ± standard error (SE). DBH Diameter breast height, H Tree height. L L gmelinii monocultures, LB L. gmelinii and B. platyphylla mixed plantations, P P sylvestris var mongolica monocultures, PB P sylvestris var. mongolica and B. platyphylla mixed plantations, N Natural regeneration forests. Different uppercase letters within a column indicate significant differences (P < 0.05) among different forest types. Significant differences were conducted based on one-way ANOVA followed by Tukey's post hoc, "***" represent a statistical significance at P < 0.001

	Season	BD (g cm $^{-3}$)	STP (%)	TC (g kg $^{-1}$)	SOC (g kg $^{-1}$)	TN (g kg ⁻¹)	C:N ratio	$\rm NH_4$ (mg kg $^{-1}$)	NH_4 (mg kg ⁻¹) NO ₃ (mg kg ⁻¹) ST (°C)	ST (°C)	SM (%)
	May	0.53±0.05Aa	71.55±2.64ABa	74.74±21.59Ba	49.46±12.43Ba	3.44±1.11Ba	22.11±1.46Ab	4.11 ± 0.44ABa	0.63±0.02Aa	4.85±0.22Ac	21.79±1.12Aa
	ylul	0.61 ±0.06ABa	63.10±1.47ABb	72.35±27.89ABa	60.49±16.57ABa	3.15±0.98Aa	22.02±1.58ABb	3.77±0.73ABa	0.67±0.06Aa	13.69±0.24Ba	18.05±1.25Ab
	September	0.55±0.03Aa	65.37±2.21Bab	77.88±0.97BCa	46.96 ± 2.01 Ba	2.49±0.11Ba	31.4±1.42ABa	3.05±0.28Ba	0.57±0.01Aa	11.75±0.22Ab	20.15±1.12ABab
LB	May	0.53±0.09Aa	69.02±2.52Bab	92.07±25.57Ba	57.09±6.83Ba	5.04±1.52Ba	18.95±1.57Aa	4.90±1.14Aa	0.39±0.04Ba	4.01±0.24Bc	21.13±1.06Aa
	ylul	0.48±0.08Ba	63.72±1.23ABb	95.06±16.05Aa	81.75±17.09Aa	4.96±0.88Aa	20.15±4.51ABa	5.27 ± 0.94Aa	0.85±0.25Aa	13.19±0.27Ca	18.17±1.18Aa
	September	0.35±0.07Ba	75.56±3.90Aa	86.84±6.97Ba	45.02±2.47Ba	3.20±0.38Ba	27.51±1.82ABa	4.15±0.51Aa	0.60±0.01Aa	$11.18 \pm 0.24 Bb$	20.42±1.06ABa
Р	May	0.63±0.04Aa	64.85±0.95Ba	54.46±5.61Ba	37.21±3.90Ba	2.69±0.21Ba	20.24±0.88Ab	2.22±0.26Ba	0.64±0.11Aa	4.15±0.29Bc	21.10±0.99Aa
	ylul	0.71±0.03Aa	55.23±4.27Ba	$38.95 \pm 0.81 Bb$	33.57±0.82Ba	2.68±0.13Aa	14.62±0.89Bc	3.70±0.73ABa	0.90±0.19Aa	15.86±0.33Aa	13.29±1.11Cb
	September	0.62±0.01Aa	63.93±1.96Ba	66.82±2.52BCa	43.55±4.80Ba	1.93±0.15Bb	34.9±1.54Aa	3.00±0.25Ba	0.59±0.04Aa	11.28±0.29ABb	20.06±0.99Ba
PB	May	0.46±0.03Aa	71.20±1.26ABa	93.47 ± 19.95Ba	76.66±6.67Ba	4.66±0.97Ba	22.05 ± 4.81 Aa	3.36±0.58ABa	0.51 ±0.06ABa	3.99±0.29Bc	20.30±1.12ABa
	July	0.55±0.06ABa	64.39 ± 2.42ABb	76.53±8.80ABab	40.44±3.90Bb	4.41±0.81Aa	18.01 ± 2.11 ABa	$3.40 \pm 0.69 \text{ABa}$	0.73±0.11Aa	15.54±0.33Aa	14.97±1.26Bb
	September	0.50±0.04Aa	67.50±1.39 Bab	55.92±3.22Cb	29.04±0.44Cb	2.01 ±0.19Ba	28.06±1.5ABa	2.74±0.14BCa	0.62±0.08Aa	11.51±0.29ABb	21.60 ± 1.12Aa
z	May	0.25±0.06Bb	76.84±3.05Aa	246.87 ± 20.90Aa	164.05 ± 16.91Aa	9.70±0.49Aa	25.36±0.94Aa	2.42±0.58Ba	0.45 ± 0.04 ABa	3.24±0.20Cb	18.64±0.84Ba
	July	0.46±0.03Ba	71.96±3.01Aa	109.94±13.18Ab	81.65±12.80Ab	4.29±1.33Ab	29.35±6.09Aa	2.44 ±0.25Ba	0.59±0.08Aa	9.01 ± 0.22Da	14.47±0.94BCb
	September	September 0.20±0.04Cb	77.67 ± 2.00Aa	144.71 ± 10.56Ab	77.12±2.70Ab	6.44±1.25Aab	23.45±2.46Ba	1.96±0.20Ca	0.47 ± 0.04 Aa	8.55±0.20Ca	18.11±0.84Ca
ANOVA	Forest	F=17.97***	$F = 12.78^{***}$	$F = 28.13^{***}$	F=24.64**	$F = 12.08^{***}$	F = 13.83 ***	F=7.52***	F = 1.57	F=183.49***	F=10.83***
	Season	F=6.49**	$F = 12.20^{***}$	F=7.59**	F=11.64**	F=6.39**	F = 1.12	F = 1.98	$F = 6.92^{**}$	F=594.17***	F=7.90**
	F×S	F = 1.36	F=1.18	F=4.96**	F=6.77**	F = 2.26	$F = 3.16^{*}$	F = 0.50	F = 0.76	F=42.86***	F=3.91**

Table 2 Two-way ANOVA showed the effect of forest type and season on soil physicochemical properties

different seasons in the same forest type

Significant differences were conducted based on two-way ANOVAs followed by Tukey's post hoc, "*,""**," and "***" represent a statistical significance at P<0.05, P<0.01, and P<0.001, respectively

According to the results of the two-way ANOVA, the interaction between forest type and season influenced TC, SOC, C:N ratio, ST, and SM (P<0.05, Table 2). Forest type affected all soil physicochemical indices except NO₃ (P<0.05), while season affected all soil variables except C:N ratio and NH₄ (P<0.05). Soil under *P. sylvestris* var. *mongolica* monocultures had the maximum BD (mean: 0.65 g cm⁻³) and minimum STP (mean: 61.34%) among the forest types, while soil under naturally regenerated forests showed the opposite pattern (mean BD: 0.30 g cm⁻³, mean STP: 75.49%). Soil under naturally regenerated forests generally had relatively high TC, SOC, and

TN contents but relatively lower ST and SM compared to artificial regeneration forests.

The litter yields under mixed plantations (LB: 2666.22 ± 313.69 kg ha⁻¹, PB: 2880.41 ± 325.74 kg ha⁻¹) and monocultures (L: 2103.89 ± 217.19 kg ha⁻¹, P: 1740.74 ± 210.61 kg ha⁻¹) were higher than those under naturally regenerated forests (894.54 ± 211.48 kg ha⁻¹) (P < 0.05, Fig. 1A). Mixed plantations increased the litter yield compared to monocultures. In addition, the litter in the *L. gmelinii* plantations (L and LB) had a higher annual decay rate than that in the other three forest types (P, PB, and N) (P < 0.05, Fig. 1B).

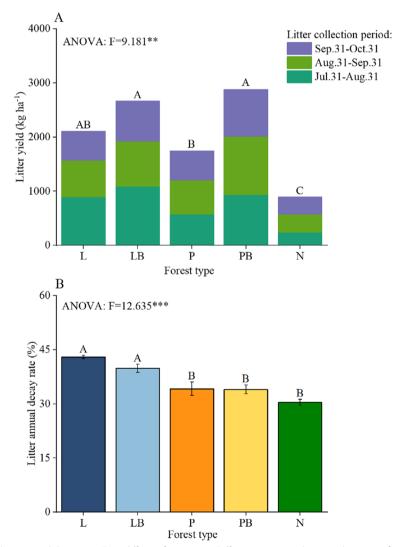


Fig. 1 Litter yield (**A**) and litter annual decay rate (**B**) in different forest types. Different uppercase letters indicate significant differences (*P* < 0.05) among different forest types. "**" and "***" represent statistical significance at *P* < 0.01 and *P* < 0.001, respectively. L for *L. gmelinii* monocultures; LB for *L. gmelinii* and *B. platyphylla* mixed plantations; P for *P. sylvestris* var. mongolica monocultures; PB for *P. sylvestris* var. mongolica and *B. platyphylla* mixed plantations; N for natural regeneration forests. Similarly hereinafter

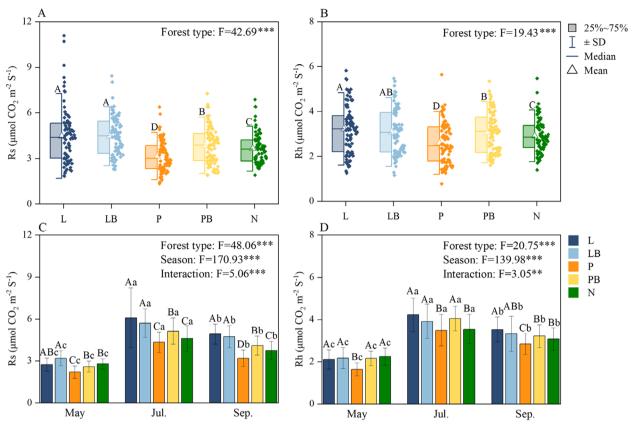


Fig. 2 Rates of soil total respiration (Rs) (A, C) and heterotrophic respiration (Rh) (B, D) in different forests. Different uppercase letters indicate significant differences (P < 0.05) among different forest types in the same season, and different lowercase letters indicate significant differences among the three seasons in the same forest type

Effects of different forest types and seasons on soil respiration

Rs and Rh varied among different forest types regardless of seasonal effects (P < 0.001, Fig. 2A–D). The average Rs values under the different forest types were 4.47 µmol $CO_2 m^{-2} S^{-1}$ (L), 4.46 µmol $CO_2 m^{-2} S^{-1}$ (LB), 3.16 µmol $CO_2 m^{-2} S^{-1}$ (P), 3.86 µmol $CO_2 m^{-2} S^{-1}$ (PB), and 3.65 µmol $CO_2 m^{-2} S^{-1}$ (P) (Fig. 2A). The average Rh values under the different forest types were 3.22 µmol $CO_2 m^{-2} S^{-1}$ (L), 3.08 µmol $CO_2 m^{-2} S^{-1}$ (LB), 2.60 µmol $CO_2 m^{-2} S^{-1}$ (P), 3.08 µmol $CO_2 m^{-2} S^{-1}$ (PB), and 2.91 µmol $CO_2 m^{-2} S^{-1}$ (N) (Fig. 2B). Compared to naturally regenerated forests, the regeneration patterns L, LB, and PB increased the Rs and Rh, while pattern P decreased the Rs and Rh (P < 0.05, Fig. 2A, B). The average Rs and Rh reached the maximum in L and the minimum in P.

Forest type, season, and the interaction between forest type and season had significant effects on both Rs and Rh (P<0.001, Fig. 2C, D). The variations in Rs and Rh among distinct forest types exhibit a consistent pattern across the three seasons: the levels of Rs and Rh consistently reach their lowest in P and peak in either L or LB. The Rs

and Rh of all forest types showed similar seasonal trends, with the maximum in July and the minimum in May. For each forest type, the mean Rs and Rh in July were more than 1.65 times and 1.59 times higher than those in May, respectively. LB had higher Rs and Rh than L only in May.

Heterotrophic respiration was the dominant part of soil total respiration for all forest types (68.84% ~ 90.20%, Table 3). Only the forest type affected the contribution of Rh to Rs (P<0.05). Mixed plantations (LB, PB) generally reduced the proportion of heterotrophic processes in total respiration compared to monocultures (L, P). Among all types of forest stands, the contribution rate of Rh to Rs was consistently the lowest in *L. gmelinii* and *B. platyphylla* mixed plantations.

Response to soil temperature and soil moisture as predictive variables of soil respiration

The van't Hoff exponential model was ultimately selected to establish the regression relationship between soil respiration and soil temperature (Fig. 3A, B) after comparing the fitting results of three classical empirical models (Table S3). The van't Hoff exponential model had a higher

 Table 3
 Contributions of soil heterotrophic respiration (Rh) to soil total respiration (Rs)

Forest types	Contribution of Rh to Rs (%)					
	May	July	September			
L	77.12±2.11 ABa	73.99±3.22 Aa	72.29±1.84 Ca			
LB	68.84±2.59 Ba	71.07±4.12 Aa	71.69±3.44 Ca			
Р	75.83±2.44 ABb	81.04±2.84 Aab	90.20±2.43 Aa			
PB	84.01±2.09 Aa	80.45±2.71 Aa	79.30±2.19 BCa			
Ν	80.58±2.09 Aa	78.44±2.86 Aa	82.58±1.89 ABa			
Two-way ANOVA	Forest type: $F = 3.03^*$	Season: <i>F</i> = 1.05	Interaction: F=0.69			

L L. gmelinii monocultures, *LB L. gmelinii* and *B. platyphylla* mixed plantations, *P P. sylvestris* var. *mongolica* monocultures, *PB P. sylvestris* var. *mongolica* and *B. platyphylla* mixed plantations, *N* Natural regeneration forests. Different capital letters within a column indicate significant differences (P < 0.05) among different forest types in the same season, and different lowercase letters within a line indicate significant differences (P < 0.05) among different seasons in the same forest type

Significant differences were conducted based on two-way ANOVAs followed by Tukey's post hoc, "*" represent a statistical significance at P < 0.05

total R^2 value compared to the Arrhenius model and a simpler equation compared to the Kucera and Kirkham model (Table S3). *L. gmelinii* monocultures had relatively low levels of Rs and Rh when the soil temperature was below 6.33 °C and 7.54 °C, respectively. With the increase in soil temperature, the Rs and Rh increased rapidly and became the highest among the forest types when the soil temperature was above 14 °C (Fig. 3A, B). The Rs and Rh under regeneration patterns P and PB were at low levels compared to the other patterns under the same soil temperature conditions.

 Q_{10} was calculated based on the parameter b in the van't Hoff exponential model (Table S4). The sensitivities of Rs and Rh to temperature under different forest types ranging from large to small were 2.316 (L) > 2.096 (N) > 1.840 (LB) > 1.716 (P) > 1.665 (PB) and 2.226 (L) > 1.878 (N) > 1.804 (LB) > 1.716 (PB) > 1.699 (P), respectively. In addition, the Q_{10} of Rs had a higher value compared to the Q_{10} of Rh under all forest types except for PB.

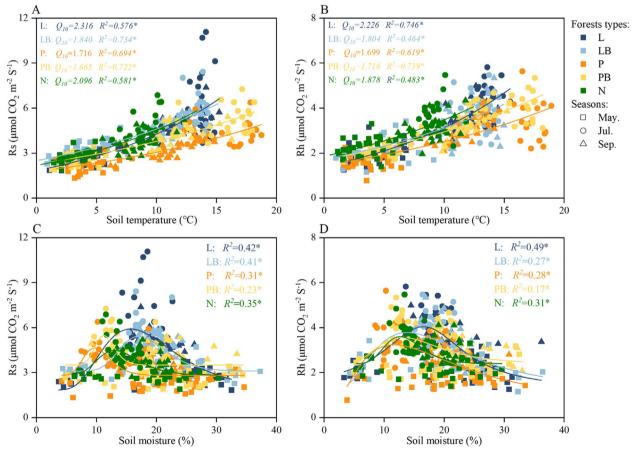


Fig. 3 Relationship between soil respiration rate (Rs and Rh) and soil temperature (**A**, **B**) as well as soil respiration rate (Rs and Rh) and soil moisture (**C**, **D**). Q_{10} is the temperature quotient calculated by the van't Hoff exponential model. R^2 is the determination coefficient of the soil respiration rate to the soil moisture regression mode

The log–normal function fitted to the regression relationship between soil respiration (Rs and Rh) and soil moisture under all forest types except for Rh under *L. gmelinii* monocultures, which was best fitted by the Lorentz function (Fig. 3C, D). However, all regression curves belonged to a unimodal curve type, indicating that the crest value of each curve represented the optimum soil moisture for soil respiration. The soil respiration increased with soil moisture up to the optimum value and then declined (Fig. 3C, D). The optimum soil moisture for Rs and Rh under different forest types ranging from large to small was 17.15% (LB) > 15.61% (L) > 12.91% (LB) > 12.88% (PB) > 12.60% (N) > 10.96% (P), respectively.

Relative contributions of environmental variables to soil respiration

Considering the significant variability in soil variables and soil respiration among different seasons, we performed PLS-PM separately for each season (Fig. S3A, B, C) and for all seasons (Fig. S3D). Environmental variables, except for forest productivity and substrate supply, showed different effects on Rs in a single season and overall seasons. Forest productivity consistently had a positive impact on Rs, whereas substrate supply had a negative effect. Nevertheless, the impact of tree density on forest productivity was negative (Fig. S4). For soil texture, an increase in the proportion of sandy soil had a negative effect on Rs, while an increase in the proportion of clay soil had a positive effect on Rs, except for September (Fig. S3, S4). Soil bulk density had a negative effect on Rs during a single season, but it had a positive effect when considering the entire season. Conversely, soil porosity had the opposite effect on Rs to that of bulk density. Soil moisture showed a positive effect on Rs in July and September but a negative effect in May and the entire seasons. The C:N ratio and soil temperature had negative and positive effects on

effects were not observed. The total effects of forest productivity, soil texture, soil bulk density, soil moisture, soil porosity, substrate supply, C:N ratio, and soil temperature on Rs were shown by the sum of direct and indirect effects (Fig. 4, Fig. S5). In May, substrate availability and soil texture emerged as the predominant factors influencing soil respiration. Shifting to

Rs, respectively, except for July and May, where these

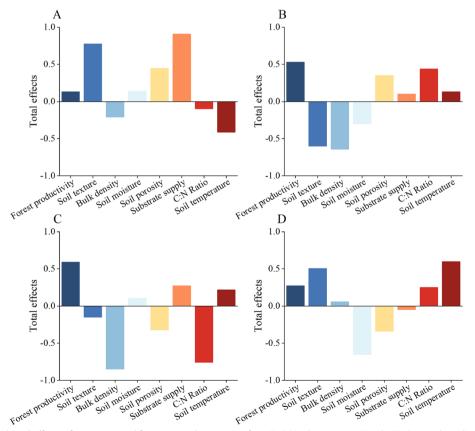


Fig. 4 Standardized total effects of environmental factors on soil respiration from PLS-PM during May (A), July (B), September (C), and the three season (D)

July, it was soil texture and soil density that took the lead in impacting this process. By September, soil density and the C:N ratio became the key determinants of soil respiration. When considering the entire seasonal span, soil temperature and moisture content stood out as the most influential factors on soil respiration.

Discussion

Effects of forest types on soil respiration

We found that not all artificially regenerated forests have increased soil respiration rates; for example, the P. sylvestris var. mongolica monocultures have reduced Rs and Rh compared to naturally regenerated forests (Fig. 2), which was inconsistent with our first hypothesis. Soil respiration is closely related to the supply of organic substrates (Ao et al. 2013), as belowground organic substrates drive the activities of plant roots and soil microorganisms. Respiratory release of CO₂ results from the breakdown of carbon-based organic substrates (Luo and Zhou 2006a). Soil respiration had a widely positive correlation with the standing stock of SOC across different ecosystems (Franzluebbers et al. 2001). In this study, the soil organic carbon stocks mainly came from two sources: the decomposition of the burning residues in the soil caused by the wildfire and the carbon input from the regenerated forest through photosynthetic carbon channeling, litter decomposition, and dead roots (Wan and Luo 2003).

The remnants of char and partially burned material could be the key factor contributing to the higher levels of SOC and TC in naturally regenerated forests, surpassing those found in monoculture and mixed forests (Table 2). The naturally regenerated sites, which have not been subjected to the land preparation procedures, could potentially exhibit a more substantial accumulation of char and partially burned material in contrast to those found in artificially regenerated forests. The soil under P. sylvestris var. mongolica monocultures had the lowest SOC stock among the forest types (Table 2), which might be one of the reasons why it had the minimum soil respiration (Fig. 2). The differences in SOC stocks of different forest types might arise from litter decomposition and humification processes (Melillo et al. 1989). Most deciduous trees usually have a faster litter decomposition rate than conifers, and mixed forests facilitate litter decomposition (Lin et al. 2021; Wang et al. 2018). In addition, soil under coniferous vegetation had more recalcitrant litter moieties, such as cutin acids, and higher accumulation of microbial synthates compared to deciduous vegetation (Quideau et al. 2001). As a consequence, soil under forests regenerated by patterns P and PB might have more stable organic compounds compared to regeneration patterns L and LB, making it difficult for soil microorganisms to catabolize (Numa et al. 2021).

As the dominant pathway of nutrient return from forests to soil (Krishna and Mohan 2017), litter decomposition provides substantial amounts of carbon substrate for soil heterotrophic respiration (Bond-Lamberty et al. 2018). Therefore, the characteristics of litter, such as yield and decay rate, have a further effect on the quantity and composition properties of the substrate (Page-Dumroese et al. 2021). In this study, different forest types accompanied by disparate species compositions had multiple litter yield and decomposition traits (Fig. 1). The litter annual decay rate had a positive effect on soil respiration (Xiao et al. 2014; Zhang et al. 2016). Litter in boreal forests had a slower decomposition rate compared to temperate and tropical forests (Krishna and Mohan 2017), forming abundant acidic crude humus at the surface soil with litterfall year after year. Although litter yields varied among different forest types (P < 0.05, Fig. 2A), there was enough litter on the ground in each forest type, making the decomposition rate a key constraint on organic carbon input.

Soil respiration in the forests regenerated by patterns L and LB was always higher than that in the forests regenerated by patterns P and PB (Fig. 2), which can be explained by the higher root biomass values (Jian et al. 2022). Plant roots not only perform autotrophic respiration continuously by consuming photosynthates but also regulate the nutrient supply for microbial metabolism by root exudate or decomposition pathways, which further affects the heterotrophic process (Luo and Zhou 2006a). As a shallow-root tree, *L. gmelinii* has interlacing root systems in the topsoil layer (Liu et al. 2021a), while *P. sylvestris* var. *mongolica* usually has more lateral roots in the deeper soil (Zhang et al. 2021).

Seasonal variation in soil respiration

We observed seasonal variation in both Rs and Rh (P < 0.05, Fig. 2C, D), similar to most other ecosystems (Chen et al. 2023; Kumar et al. 2023). Overall, soil respiration in July was significantly higher than that in September and May for all forest types. In the growing season, higher temperatures conducive to plant growth could also benefit soil microbial metabolic activity (Keidel et al. 2015). ST and SM frequently serve as crucial factors in regulating seasonal variation in soil respiration on a global scale (Raich et al. 2002). In this study, ST had a higher \mathbb{R}^2 of regression with soil respiration compared to SM (Fig. 3), indicating that soil respiration responds to temperature changes more directly than moisture. Although ST is recognized the primary factor regulating soil respiration, with SM being secondary (Laganière et al. 2012), SM often plays a dual role in the process affecting soil respiration. SM is not only a crucial participant in the decomposition process, but it also serves as a pivotal determinant of soil thermal conductivity (Abu-Hamdeh 2003). This conductivity is an essential attribute of soil, governing the dynamics of heat transfer and retention throughout the soil layers and ultimately determining soil respiration (Meyer et al. 2018).

The disparate seasonal patterns of soil respiration in different forest types can be explained by their diverse plant communities (Grogan and Chapin Iii 1999; Shabaga et al. 2015). The rhizosphere labile C supply from photosynthesis contributes 10-90% to total soil respiration depending on the seasons of the year (Hanson et al. 2000; Raich et al. 2002). There is a stronger seasonal variation in rhizosphere labile C supply than in soil organic matter or aboveground litter and dead root decomposition (Wan and Luo 2003). Soil respiration under regeneration patterns L and LB had larger seasonal coefficients of variation compared to regeneration patterns P and PB (Fig. 2A, B), which might be related to the phenological properties of the dominant tree species. The deciduous species L. gmelinii and evergreen species P. sylvestris var. mongolica had disparate seasonal patterns of productivity, leaf longevity, root growth, root turnover, and litterfall (Schulze 1982). Root respiration and part of soil microbial respiration largely depend on the amount of photosynthates translocated from the aboveground leaves (Högberg et al. 2001). Consequently, these parts of soil respiration would be more sensitive to seasonal changes in photosynthate activity under regeneration patterns L and LB, as photosynthate activity under deciduous forests had a greater seasonal variation compared to evergreen forests under the same climatic conditions (Curiel yuste et al. 2004).

Rs under mixed plantations had lower Q_{10} values compared to monocultures (Fig. 3A), which can be explained by the higher tree densities in the former (Han et al. 2020). The naturally regenerated of *B. platyphylla* within canopy gaps resulted in the tree density under mixed plantations being 1.4 times higher than those under monocultures (Table 1). In addition, the heterogeneous structure of seedling establishment under naturally regenerated forests might also contribute to increasing their Q_{10} values. Unlike plantations where the vegetation regenerated artificially was relatively homogeneous, postfire naturally regenerated stands usually showed an obvious "block" regeneration pattern due to the insufficient seed supply from adjacent unburned trees (Harvey et al. 2016). In fact, despite more than 30 years of naturally regenerated, there were still patches without trees established under the naturally regenerated forests in this study.

Mediation of soil properties on soil respiration

The PLS-PM results indicated that soil temperature and moisture are the primary determinants of soil respiration throughout the broader seasonal shifts (Fig. 4D). However, for a single season, forest productivity and soil properties—such as soil texture, substrate availability, bulk density, and the C:N ratio—have a greater impact on soil respiration (Fig. 4A-C), thus supporting our second hypothesis.

Soil respiration is interactively affected by multiple environmental variables and often responds to the most limiting factor. Soil temperature and moisture usually play a decisive role in regulating soil respiration on a global scale (Tang et al. 2020). During the seasonal transitions in northern forests, soil temperature and moisture levels stand out as the most pronounced environmental variables. Yet, within the span of an individual season, fluctuations in these factors might be less pronounced, thereby highlighting the pivotal role of soil properties in modulating the soil respiratory. In May, substrate supply and soil texture were the dominant factors influencing Rs (Fig. 4A). Substrate supply provides the fundamental material basis for soil respiration (Liu et al. 2006), as one CO₂ molecule released by soil respiration indicates that one organic substrate is consumed. The categorization of soil texture typically hinges on the proportionate presence of particles with varying sizes within the soil matrix, encompassing coarse sand grains, fine silt particles, and the minute clay particles. The distinct assemblages of soil textures can significantly influence the soil physical characteristics, including its aeration and capacity to retain moisture, properties that subsequently have a bearing on the process of soil respiration (Cable et al. 2008).

Soil bulk density emerged as the predominant factor affecting Rs in July and September (Fig. 4B, C). The soil bulk density is dictated by its texture, a characteristic that is itself shaped by the soil structural composition (Martín et al. 2017). The decrease in soil porosity with the increasing soil bulk density could reduce soil moisture, which further influences soil respiration by affecting the transport of water, O₂, and CO₂ in the soil (Luo and Zhou 2006a). Soil bulk density, as a fundamental property of soil, is closely related to other physicochemical properties. For instance, soil bulk density can also affect soil respiration by influencing soil organic carbon content, C:N ratio, and soil thermal properties (Abu-Hamdeh 2003). Variations in soil bulk density across different forest types could be attributed not only to the distinct preparatory practices conducted prior to afforestation but also potentially to the divergent vegetation that emerges following the fire (Weng et al. 2021). The plant canopy could change the temperature and moisture in the soil layer by controlling the receipt, exchange, and redistribution of solar radiation, heat, and precipitation, which further affects soil respiration (Tanaka and Hashimoto 2006). Artificially regeneration forests had more mature canopies compared to naturally regenerated forests (Table 1), as forests regenerated with artificial participation recovered significantly faster than naturally regenerated forests (Chen et al. 2014).

C:N ratio was the second most important factor influencing Rs in September (Fig. 4C). C:N ratio had a negative impact on Rs, which is consistent with the research finding of Yang et al. (2022). The C:N ratio plays a crucial role in determining the speed at which microbes decompose carbon, release nutrients from organic matter to plants, and produce stable soil carbon compounds. This elevated C:N ratio emerges as a critical factor that constrains soil respiration. The optimum C:N ratio of the organic material in healthy soil is reported to vary between 20:1 and 30:1. Typically, a higher C:N ratio may imply a slower rate of organic carbon decomposition. This is mainly because microorganisms require nitrogen to meet their metabolic needs during the decomposition of organic matter. An increased C:N ratio may signal an insufficient nitrogen supply, leading to reduced microbial activity and, as a result, a slower rate of soil respiration. Throughout the growing season, as plants and microbes assimilate nitrogen from the soil, there is a widespread escalation in the C:N ratio in forest soils by September. Nevertheless, in the decomposition of organic materials, the C:N ratio is shaped not only by the availability of nitrogen but also by the prevailing quantities and varieties of carbon in the substrate, which play a pivotal role in regulating the C:N ratio and Rs (Schmidt et al. 2011).

Conclusions

Regeneration patterns exerted varying effects on soil respiration. Specifically, mixed species plantation regeneration demonstrated an improvement in soil respiration compared to naturally regenerated forests. However, the impact of monocultures on soil respiration was contingent upon the tree species involved. In addition, mixed plantations had a lower temperature sensitivity of soil respiration than their respective monocultures. Soil temperature and moisture dominated the influence factors on soil respiration throughout the broader seasonal shifts. However, for a single season, forest productivity and soil properties-such as soil texture, substrate availability, bulk density, and the C:N ratio-have a greater impact on soil respiration. This might be due to the diverse soil conditions shaped by different forest types through various pathways such as litter, root, and canopy, during the long postfire renewal process of plants.

Abbreviations

- L Larix gmelinii Monocultures
- LB L. gmelinii and Betula platyphylla mixed plantations
- P Pinus sylvestris Var. mongolica monocultures
- PB *P. sylvestris* Var. *mongolica* and *B. platyphylla* mixed plantations
- N Naturally regenerated forests

- Rh Soil heterotrophic respiration
- Rs Soil total respiration
- Q_{10} The sensitivity of soil respiratory processes to temperature
- BD Soil bulk density
- STP Soil total porosity
- TC Soil total carbon
- TN Soil total nitrogen
- SOC Soil organic carbon NH₄ Soil ammonium nitrogen
- NO₂ Soil nitrate nitrogen

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-024-00325-4.

Additional file 1: Fig. S1 Soil heterotrophic respiration determination based on the trenching method. The trenches were dug to a depth of about 50 cm (20 cm below the rooting depth) around the subplots (A-D). The trenches were backfilled after lining with double layers of polyethylene sheet to prevent root ingrowth (E). Living plants inside each subplot were clipped at the soil surface and the clipped plant materials were left in the subplots (F). All the subplots were completed in September 2021. Fig. S2 The determintion of litter field and litter annual decay rate. The litter collection mesh nets were 1 m x 1 m (A). The initial decomposition material in each bag was 5 g oven-dried fresh litter collected in September 2021 (B). The litter bags were placed in the litter layer of each plot in September 2021 (C) and retrieved in September 2022 (D). Fig. S3 Partial Least Squares Path Modeling (PLS-PM) of soil respiration (Rs) in forests with different postfire regeneration patterns during May (A), July (B), September (C), and the three season (D). The one-way arrows represent the hypothesized direction of causation. The red and blue arrows represent negative and positive flows of causal relationships, respectively. R2 is the coefficient of determination of the endogenous latent variables, which indicates the amount of variance in the endogenous latent variable explained by its independent variables. The goodness-of-fit (GoF) is calculated as the geometric mean of the average communality and the average R2 value, which assesses the overall prediction performance of the model. Category forest productivity includes forest basal area, stand volume, tree density, and litter annual decay rate. Category soil structure includes the percentages of sand, silt, and clay soil. Category substrate supply includes the contents of soil total carbon, total nitrogen, organic carbon, ammonium nitrogen, and nitrate nitrogen. Fig. S4 Visualizing the loadings (correlations) of the different categories. The bule and red arrows represent the positive and negative effects of the internal variables on the outer categories, respectively. Fig. S5 Standardized indirect (A-D) and indirect (E-H) effects of environmental factors on soil respiration from PLS-PM during May (A, E), July (B, F), September (C, G), and the three season (D, H). Table S1 The basic situation of the three study sites. Table S2 The soil structure and texture information under forests with different postfire regeneration patterns across May, July, and September. Table S3 The determination cofficients (R2) of different regression models between soil respiration and soil temperature under different forest types. Table S4 Parameters in the van't Hoff exponential model of the relationship between soil respiration rate (μ mol CO₂ m⁻² S⁻¹) and soil temperature (°C) in different forest types.

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Authors' contributions

Fangyuan Shen and Lixue Yang conceived and designed the research; Fangyuan Shen, Chengfeng Shan, Siyu Zhou, and Huifeng Liu performed the experiments and analyzed the data; Fangyuan Shen, Chengfeng Shan, Lixue Yang, and Yuchun Yang wrote and edited the manuscript.

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Availability of data and materials

The datasets used and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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