



Soil priming effect and its response to nitrogen addition in regional and global forests: Patterns and controls

Peng Tian^{a,b}, Shengen Liu^c, Biao Zhu^d, Qingkui Wang^{a,b,*}

^a School of Forestry & Landscape Architecture, Anhui Agricultural University, Hefei 230036, China

^b Huitong Experimental Station of Forest Ecology, CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Shenyang 110016, China

^c College of Biological and Pharmaceutical Sciences, China Three Gorges University, Yichang 443002, China

^d Institute of Ecology, College of Urban and Environmental Sciences, and Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, Beijing 100871, China

ARTICLE INFO

Keywords:

Priming effect
Nitrogen addition
Inhibition effect
Geographic pattern
Forest ecosystem

ABSTRACT

Although the priming effect (PE) of soil organic matter mineralization and its response to nitrogen (N) amendment are widely studied in terrestrial ecosystems, great uncertainties in their geographic patterns constrain the establishment of advanced climate-carbon (C) model. By combining a laboratory experiment incubating soils from nine temperate forests in China with a meta-analysis of 32 publications across global forests, we tested the PEs and their response to N addition to explore their geographic patterns and the potential determinants. We found a weak dependence of the PE on latitude and mean annual temperature (MAT) in temperate forests in China, but a significant dependence of the PE on MAT across global forests after controlling for the exogenous C quantity. Soil pH was evidenced to control the geographic patterns of the PE. Consistent with meta-analysis, a general inhibition impact of mineral N addition on PE was detected in the laboratory experiment, ranging from -5.50 to 228.41% . In contrast with an inapparent dependence on MAT at the global scale, N inhibition effect in incubation experiment was experimentally detected to negatively correlate with MAT. Increase in soil N availability basically attenuated the response of PE to N addition. Across the globe, the PE and N inhibition effect in coniferous forests were more sensitive to latitude than those in broadleaved forests. Overall, our results uncovered distinct patterns but consistent controls of PE and N inhibition effect between the regional and global scales, and emphasized the importance of considering forest type in predicting soil C dynamics in response to global change.

1. Introduction

Soil contains the largest active organic carbon (C) pool in terrestrial ecosystems, storing approximately 1500 Pg C in the top 1 m layer (Scharlemann et al., 2014). The mineralization of soil organic C (SOC), serving as one of the major fluxes in soil C dynamics, releases 60–98 Pg C to the atmosphere as CO₂ every year (Bond-Lamberty and Thomson, 2010; Pan et al., 2011). In field, the mineralization of SOC can be modified by the addition of exogenous C such as plant litter and root exudates, which is termed as the priming effect (PE; Kuzyakov et al., 2000). Although the PE is recognized to be widespread in terrestrial ecosystems and widely studied, the pattern of the PE at a large scale and its controls are poorly understood (Bastida et al., 2019; Liu et al., 2020; Perveen et al., 2019). Numerous non-uniform experimental settings,

measurements and result presentations are used, making cross-study comparisons difficult and hindering broad-scale generalizations (e.g., Di Lonardo et al., 2018; Tian et al., 2019a; Tian et al., 2019b). Clarifying soil C dynamics is an essential precondition for the enhancement of soil C sink and realization of C neutrality. Therefore, systematic investigations concerning the pattern and the fundamental drivers of the PE are necessary to accurately predict the SOC dynamics.

Across previous investigations, the PE was demonstrated to vary greatly in soils with contrasting properties (Chen et al., 2014; Chen et al., 2018; Davidson et al., 2016; Paterson and Sim, 2013). Soil N availability was broadly suggested to be a critical regulator of PE due to its mediation on microbial community and function (Kuzyakov et al., 2000; Tian et al., 2016; Zhang et al., 2013). Under current scenarios of global change, increasing active N deposition from the atmosphere are

* Corresponding author at: School of Forestry & Landscape Architecture, Anhui Agricultural University, Hefei 230036, China.

E-mail address: wqkui@163.com (Q. Wang).

<https://doi.org/10.1016/j.catena.2022.106806>

Received 10 July 2022; Received in revised form 5 November 2022; Accepted 18 November 2022

Available online 28 November 2022

0341-8162/© 2022 Elsevier B.V. All rights reserved.

demonstrated to influence soil C dynamics due to the tight coupling of C and N cycles (Mason-Jones et al., 2018; Tian et al., 2019a; Tian et al., 2019b; Wang et al., 2014). In most individual investigations, N enrichment in soil reduced the degree of positive PE (Fontaine et al., 2011; Hartley et al., 2010; Wang et al., 2014). The “N mining theory” was mostly proposed to be the underlying mechanism, which suggests that N addition reduces microbial N mining from SOC and hence the PE (Chen et al., 2014; Fontaine et al., 2011; Murphy et al., 2015). Thus, microbial response following N application should be the fundamental driver of changes in PE (Leff et al., 2015; Rousk et al., 2010). In contrast, a few studies suggested that the microbial activity is enhanced when N supply in soil matches microbial demands after fresh C input accompanying with exogenous N, consequently inducing a greater PE (Chen et al., 2014; Meyer et al., 2018). Hence the inhibition effect of N addition on PE was challenged sometimes, depriving the responses of PE to N input of universal mechanisms at a large scale.

In addition to soil heterogeneity in terms of nutrient content, vegetation type might also account for the discrepancies in the SOC priming and its response to N addition (Rasmussen et al., 2007). Generally, the quality of soil organic matter in coniferous forests is generally lower (wider C:N ratio) than that in broadleaved forests (Wang et al., 2016a; Wang et al., 2018), which alter microbial community composition and metabolism (Zhang et al., 2017), thereby indirectly affecting soil C dynamics as well as their response to N enrichment. Considerable variations in the PE and its response to N addition have been detected between coniferous and broadleaved forests in individual studies (Di Lonardo et al., 2017; Hartley et al., 2010; Maestrini et al., 2014). However, whether the geographic patterns of the SOC priming and its response to N addition differentiate in various forest types remains unclear. Clarifying the variations in soil C dynamics between coniferous and broadleaved forests is essential to accurately predict the effect of land use change in future.

Our understanding of the geographic patterns of the PE as well as their response to N addition is limited. This calls for a systematic study concerning the PE with N amendment over broad geographic scales. In the present study, soils from nine temperate forests in China were incubated with ^{13}C -labeled glucose, crossed with a mineral N amendment. To verify whether the results for China's temperate forests are applicable at the global scale, 221 observations from 32 literatures were further collected. This study aimed to 1) investigate the geographic pattern of the PE and N addition effect on PE in temperate forests in China and across the globe; 2) examine whether the inhibition of PE by N addition is applicable in both regional and global scales; and 3) uncover the potential effect of forest type on the geographic pattern of the PE and the N addition effect on PE. Clarifying these knowledge gaps would help us predict the terrestrial C cycling under global change conditions. Based on current observations, we hypothesized that N addition would reduce the degree of PE and the geographic patterns of PE and its response to N amendment would differentiate in various forest types.

2. Materials and methods

2.1. Study area

We collected soils in 9 temperate forests from 7 sites in China with a range of different ecosystems (Fig. 1). These soils span a latitudinal range from 39°57' to 51°31' N and have distinct edaphic characteristics, with mean annual temperature (MAT) ranging from -5.8 to 7.1 °C and mean annual precipitation (MAP) ranging from 468 to 947 mm (Table 1). These forests comprised broadleaved, coniferous, and coniferous-broadleaved mixed forests according to their dominant tree species.

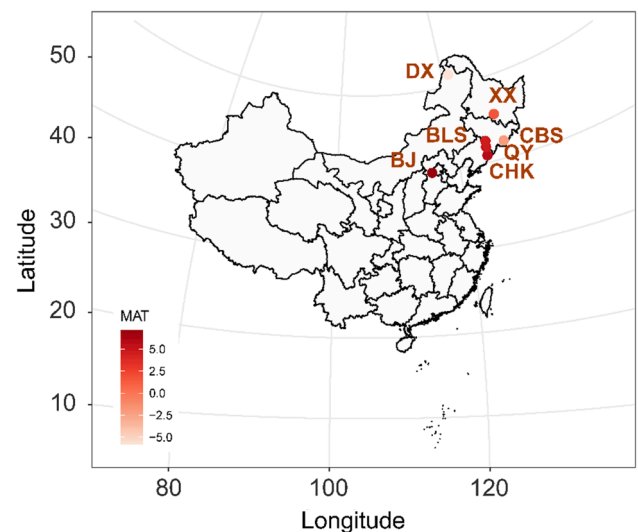


Fig. 1. Site locations of studied nine temperate forests in China.

2.2. Field sampling and soil analysis

Soil samples were collected from late July to early August in 2014. In each forest, 3 plots (100–150 m²) were established. In each plot, the upper 10 cm of mineral soil was sampled from 8 to 10 locations, and gently combined into a composite sample. All soil samples were transported with a low-temperature incubator with ice (<4 °C) to laboratory within 24 h after collection. Then, soil samples were sieved to 2 mm, and then homogenized. One part was stored at 4 °C for incubation and microbial measurement, and the rest was air-dried for chemical analysis.

The initial SOC and total N contents were measured by dry combustion using an elemental analyzer (Thermo Fisher Flash 2000, USA). Soil pH was measured with a pH meter from a soil slurry with 1:2.5 (weight/volume) soil to distilled water ratio. Soil mineral N (sum of ammonium and nitrate N) was extracted using 2 M KCl solution and determined using colorimetry (Lu, 2000). Soil total phosphorus (P) was measured colorimetrically. Available P was analyzed colorimetrically through the molybdate blue method after the soil was extracted with 1 M NH₄F solution. Exchangeable cations (K⁺, Na⁺, Ca²⁺, Mg²⁺) were determined by flame emission spectrophotometry (Hitachi Z-8100, Tokyo, Japan) (Lu, 2000).

To reveal the shift in microbial demands for substrate following exogenous C and N addition, we determined the activities of three hydrolytic enzymes, including two C-acquisition (invertase, β-glucosidase) and one N-acquisition (urease). At the end of incubation, invertase activity was determined with 35.06 mM saccharose in 2 M acetate buffer (pH 5.5) at 50 °C for 3 h. The reducing sugars released during the activity were assessed following Schinner and von Mersi (1990). β-glucosidase activity was determined by spectrophotometrically measuring the formation rate of p-nitrophenyl-β-D-glucopyranoside during a 90 min soil incubation at 37 °C and pH 6.5 (Tabatabai, 1982). Urease activity was determined taking advantage of the colorimetric determination of ammonium (Kandeler and Gerber, 1988). Phospholipid fatty acid (PLFA) analysis was performed to demonstrate microbial community structure in soil. Phospholipids were extracted from 3 g of soil fresh weight and analyzed using an Agilent 7890 Gas Chromatograph. Gram-positive bacteria were identified by the terminal and mid-chain branched fatty acids (i15:0, a15:0, i16:0, i17:0, a17:0, 10Me-17:0), and cyclopropyl saturated and monosaturated fatty acids (16:1ω7c, cy-17:0, 17:1ω8c, 18:1ω7c, cy-19:0) were considered indicative of gram-negative bacteria (Joergensen, 2022). The fatty acids 16:1ω5c, 18:1ω9c and 18:2ω6,9 were considered to represent fungal PLFA. The total PLFA concentration was calculated from the identified PLFAs (14:0, 15:0, 16:0, 17:0, 18:0, 20:4ω6,9,12,15; and those listed above).

Table 1
General characteristics of the nine forest types in temperate China.

Site	MAT (°C)	MAP (mm)	Organic C (g kg ⁻¹)	Total N (g kg ⁻¹)	C/N ratio	Total P (mg kg ⁻¹)	pH	Mineral N (mg kg ⁻¹)	Microbial biomass (nmol PLFAs g ⁻¹)	Forest type	Dominant tree species
DX1	-5.8	485	30.5	1.6	19.1	0.4	5.4	9.9	121.2	Broadleaved	<i>Betula platyphylla</i>
DX2	-5.2	468	21.5	1.6	13.7	2.6	6.2	5.2	74.4	Coniferous	<i>Larix gmelinii</i>
XX	1.6	671	64.1	5.1	12.4	1.4	5.4	19.7	196.9	Broadleaved	<i>Quercus mongolica</i> , <i>Betula platyphylla</i> , <i>Ulmus davidiana</i>
CBS	-2.1	869	29.9	1.7	17.4	0.2	5.2	21.5	105.2	Mixed	<i>Pinus koraiensis</i> , <i>Larix olgensis</i> , <i>Abies nephrolepis</i> , <i>Picea jezoensis</i> var. <i>microsperma</i>
BLS	4.6	781	32.5	2.8	11.7	0.6	5.6	18.6	142.2	Coniferous	<i>Larix olgensis</i>
QY	4.8	885	37.6	3.0	12.7	0.5	5.8	12.9	114.5	Coniferous	<i>Pinus koraiensis</i> , <i>Larix kaempferi</i>
CHK	5.7	947	23.9	1.4	17.0	0.4	6.1	15.4	90.3	Coniferous	<i>Pinus koraiensis</i>
BJ1	7.1	499	43.3	3.4	12.7	0.5	6.6	25.9	91.6	Broadleaved	<i>Quercus liaotungensis</i>
BJ2	7.1	499	34.3	2.5	14.1	0.7	6.9	31.3	61.9	Coniferous	<i>Pinus tabulaeformis</i> , <i>Larix principis-rupprechtii</i>

The ratios of fungal to bacterial (F: B) PLFA and gram-positive to gram-negative (G+: G-) bacterial PLFA were taken to represent the relative abundance metrics of these groups.

2.3. Incubation experiment and the PE calculation

Soils from each forest biome were incubated with three replications. Three treatments were included in this experiment: soil without addition (Control), soil with exogenous C addition (C), and soil with combined addition of exogenous C and N (CN). For incubation, 100 g fresh soil (oven-dried weight) were placed into 1 L Mason jars. These containers equipped with pierced lids for gas exchange, but minimized evaporation and soil drying. The soil was adjusted to 50 % of water holding capacity (WHC) and pre-incubated for 24 h in the dark at 20 °C. Then, ¹³C-labelled glucose (δ¹³C = 265 ‰) solution with or without N input (NH₄NO₃) was homogeneously added to soil surface. ¹³C-labeled glucose and NH₄NO₃ corresponds to an addition of 2 % of SOC content and 100 mg N kg⁻¹ soil, respectively. Finally, soil moisture content was adjusted to 60 % of WHC by adding distilled water and maintained by regularly adding distilled water throughout the culture. The control treatment was amended with distilled water to reach the same soil moisture content. Six additional jars without soil were incubated additionally as blanks to account for atmospheric CO₂ level. All the jars were incubated in the dark in incubators for 102 days and the temperature was adjusted to the MAT of soil original sites. To resemble the diurnal temperature dynamics, the incubator temperature gradually changed between the designed temperature plus 6 °C and minus 6 °C within 24 h.

Evolved CO₂ was collected using a syringe at days 1, 3, 5, 8, 11, 16, 21, 28, 35, 42, 57, 72, 87, and 102 after incubation. Immediately after collection, the concentration of released CO₂ and its δ¹³C value were measured using a spectroscopic stable isotope analyzer with a precision of 0.2 ‰ (Picarro G2131-i Analyzer; Santa Clara, USA). At least 150 ml of gas sample was collected from each jar to achieve a stable and precise measurement. The analyzer was calibrated with two standards each time before measurement.

To calculate the amount of CO₂-C derived from glucose and native SOC mineralization during the incubation period, the following equations were used:

$$C_G = C_T(\delta_T - \delta_S)/(\delta_G - \delta_S) \quad (1)$$

$$C_S = C_T - C_G \quad (2)$$

In the equations, C_T is the total amount of CO₂-C during the considered time interval, and δ_T is the corresponding isotopic composition; C_G is the amount of CO₂-C derived from glucose, and δ_G is the isotopic value of glucose; C_S is the amount of CO₂-C derived from SOC, and δ_S is the ¹³C abundance of respired CO₂ from the control soil.

Cumulative PE (mg CO₂-C g⁻¹ SOC) induced by the glucose addition

was calculated as:

$$PE = C_g - C_{ng} \quad (3)$$

where C_g is the cumulative amount of SOC-derived CO₂-C in treatments with glucose addition, and C_{ng} is the amount of SOC-derived CO₂-C in the same soil without labeled glucose addition.

N inhibition of PE was calculated as:

$$N \text{ inhibition effect} = (PE_C - PE_{CN})/PE_C \times 100 \quad (4)$$

where PE_C and PE_{CN} are the PE induced by solely glucose input and by concurrent addition of glucose and NH₄NO₃, respectively. Thus, positive values indicate N addition reduced the magnitude of the PE.

2.4. Data collection across global forests

To collect data of the PE and its response to N addition in the world's forests, we searched the Web of Science and China National Knowledge Infrastructure (CNKI, <https://www.cnki.net>). In this meta-analysis, we searched for relevant articles in databases (publication years 1999-Feb. 2021) using two search statements as keywords: (1) priming AND (nitrogen enrichment OR nitrogen addition OR nitrogen application OR nitrogen input OR nitrogen deposition) AND (forest); and (2) (isotope OR ¹⁴C-labeled OR ¹³C-labeled) AND (decomposition OR respiration OR mineralization) AND (nitrogen enrichment OR nitrogen addition OR nitrogen application OR nitrogen input OR nitrogen deposition) AND (forest). Literatures were further selected according to the following criteria: (i) Articles were excluded when N was added accompanying with P and/or other nutrients; (ii) Study of primed CO₂-C or SOC-derived CO₂-C using ¹³C isotope-tracing technique; (iii) Experimental treatments included the untreated control (without C substrate or nutrient addition), C substrate addition, and C substrate plus nutrient addition treatments; (iv) Means, standard deviations (SDs) or standard errors (SEs), and the number of replicates for control and treatment groups could be extracted from text, tables or digitized graphs; (v) When one study involved more than one observation from different sampling times, the latest measurements were adopted. A total of 221 records from 32 papers were finally included (Fig. S1). Soil properties (including SOC, TN, C/N, pH and texture), climatic factors (mean annual temperature, MAT; and mean annual precipitation, MAP), geographic information (longitude, latitude) associated with the corresponding sites as well as experimental operation (experimental duration, type and quantity of exogenous carbon, type and quantity of N fertilization) were also collected. In our study, two authors worked independently to extract data from eligible studies, and a third author reviewed data extraction, and resolved conflicts.

2.5. Statistical analysis

The Kolmogorov–Smirnov test was performed to check whether all data were normal. Non-normal variables were log-transformed before the analysis. A general linear model was used to explore the geographic patterns of the PE and N inhibition of PE along the gradients of latitude and MAT in temperate forests in China. Relationships between the PE or N inhibition of PE and environmental variables (geographic information, climatic factors, soil physicochemical properties, microbial community and enzyme activity) were assessed by Pearson correlation. Prior to conducting structural equation modeling (SEM), we used a random forest procedure to reduce the number of predictors that significantly explained the variation found in the PE and N inhibition of PE (geographic information, climatic factor, soil properties and microbial traits) for each dataset (Delgado-Baquerizo et al., 2016). Random forest analysis was recommended for evaluating the relative importance of the primary predictors of the environmental variables. By building bagged tree ensembles and including a random subset of features for each tree (9999 trees), random forest analysis could alleviate multicollinearity problems in multivariate analyses. Subsequently, to construct the direct and indirect pathways that environmental variables influenced the PE and N inhibition of PE, SEM was performed using the data from laboratory experiments. Predicted causal relationships were based on prior knowledge of how soil properties impact the PE and N addition effect on PE. By the stepwise removal of non-significant paths in the initial model, a final model that best fit our data was generated. To confirm the robustness of the relationships between key ecosystem factors and the PE or N inhibition of PE, we used piecewise SEM to account for random

effects of sampling sites, providing “marginal” and “conditional” contribution of environmental predictors. Fisher’s C test was used to judge the goodness of the modelling results. The models were modified stepwise according to the pathway significance ($p < 0.05$) and the goodness of the model ($0 \leq \text{Fisher's } C/\text{df} \leq 2$ and $0.05 < P \leq 1.00$).

For data of PE and N inhibition effect collected across the globe, we conducted partial correlation to evaluate the relationships between the PE or N inhibition effect and the factors given the inter-correlations among these factors. The greater the difference in the partial correlation coefficient (Pearson method) between the zero-order and controlling correlation, the stronger the effect of the factor being controlled. These statistical analyses were performed based on original data with three replicates except the general linear model, using the “nlme”, “lme4”, “psych”, “randomForest”, “rfPermute” and “piecewiseSEM” packages in R version 4.0.2 (R Core Team, 2020). Significant differences were accepted at the $p < 0.05$ level of probability.

3. Results

3.1. Geographic patterns of the PE and N inhibition of PE

Glucose addition universally induced substantial positive PE in temperate forests in China, ranging from 4.35 to 6.71 mg C/g SOC at the end of incubation (Fig. 2a). Although the PE varied significantly across forests, no apparent dependence of the PE on latitude or MAT was detected (Fig. 2a, b). The meta-analysis from 32 publications in global forests corroborated this finding apparently, with four-fifths of observations showing positive PE (Fig. S2). However, significant dependence

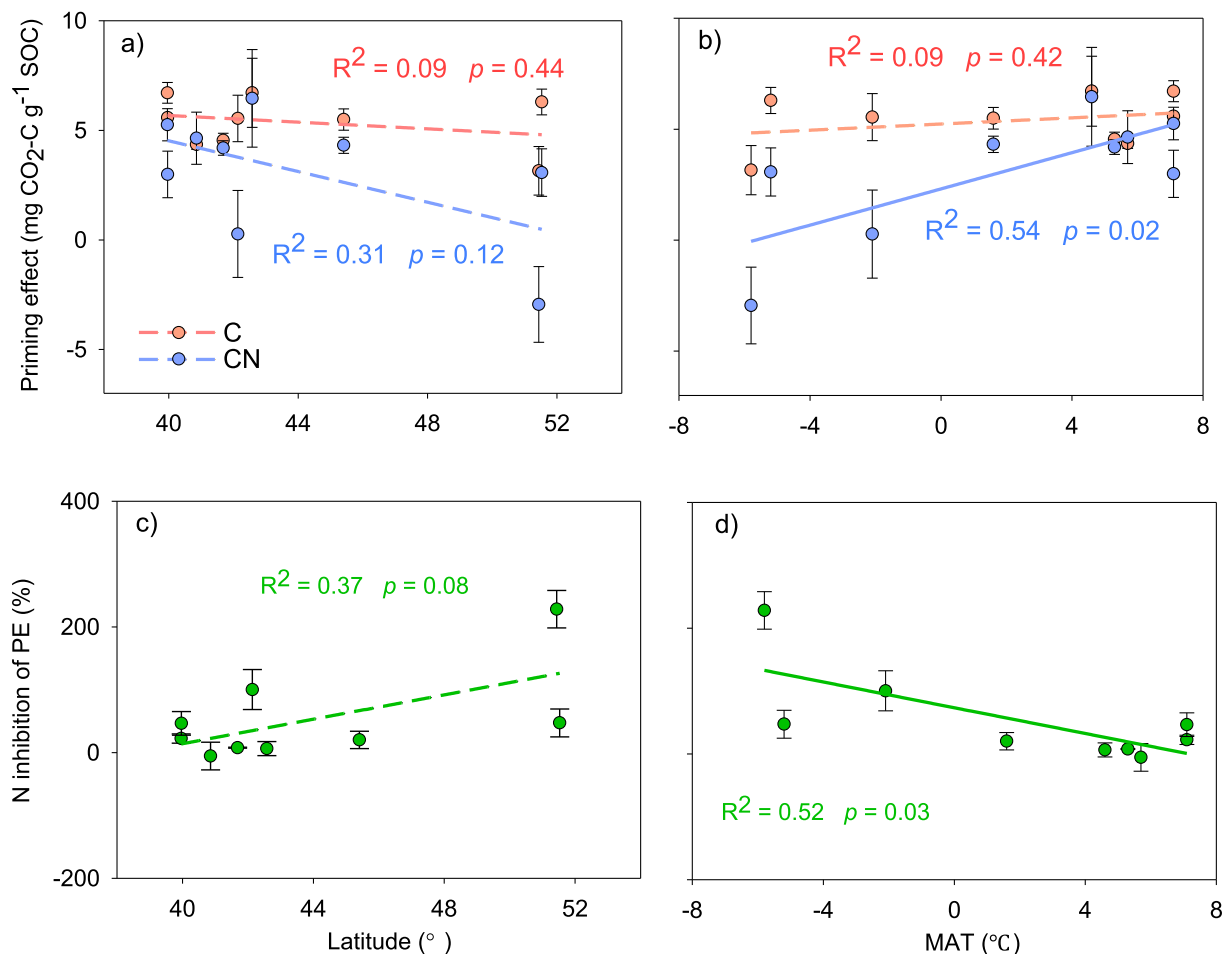


Fig. 2. Geographic patterns of the priming effect (PE) induced by glucose addition without (red) and with NH₄NO₃ (blue) addition along the gradients of latitude (a) and MAT (b); and geographic patterns of N inhibition of PE along the gradients of latitude (c) and MAT (d) in temperate forests in China.

of the PE on MAT was revealed after controlling for the exogenous C quantity (Fig. 3a). Overall, simultaneous amendments of glucose and NH_4NO_3 weakened the degree of the positive PE compared to solely glucose addition in temperate forests in China (Fig. 2a), with the relative inhibition of PE by N addition ranging from -5.50 to 228.41 %. Of the studies collected in meta-analysis, approximately two-thirds showed inhibitory effects of N enrichment on the PE (Fig. S2). The N inhibition effect decreased linearly with increasing MAT in the temperate forests in China ($R^2 = 0.52$, $p = 0.03$; Fig. 2d). Across the globe, in contrast, the MAT-dependence of N inhibition effect was absent (Fig. 3b).

3.2. Determinants of the PE and N inhibition of PE

Pearson correlation results showed that the urease and invertase activities and the ratio of fungal to bacterial PLFAs negatively correlated with the PE in temperate forests in China ($p < 0.05$; Fig. 4a). Inhibition effect of N addition on PE revealed negative relationships with MAT, soil mineral N, exchangeable Na^+ , Ca^{2+} , Mg^{2+} contents, and the ratio of gram-positive to gram-negative bacterial PLFAs, whereas correlated positively with soil C: N and available P ($p < 0.05$; Fig. 4a). To further uncover the relative importance of above variables in controlling the PE and N inhibition of PE, a random forest analysis was performed. We found that urease activity, soil pH and Mg^{2+} content were the three most important factors in regulating the PE ($p < 0.05$; Fig. 4b), while N inhibition of PE was dominantly influenced by Na^+ and Mg^{2+} contents as well as MAT ($p < 0.05$; Fig. 4c).

SEM was constructed to reveal the pathways that environmental variables impact the PE and N inhibition of PE. Taken together, our model explained 48 % of the variations in the PE, and 72 % of the variations in N inhibition of PE when considering the random effects of “sampling sites” (Fig. 5). The magnitude of the PE increased as the soil pH approached neutral, whereas pH-mediated microbial community composition and urease activity showed negative correlation with the PE (Fig. 5a). Consistent with the results of random forest model, soil pH and pH-mediated urease activity dominantly regulated the geographic patterns of PE (Fig. S3). Soil mineral N and exchangeable Na^+ contents negatively impacted the N inhibition of PE (Fig. 5b). Basically, MAT exerted a negative impact on N inhibition of PE indirectly through its positive correlations with total N and exchangeable Na^+ contents (Fig. 5b).

3.3. Impacts of forest type on the patterns of PE and N inhibition of PE

Across the globe, the changes in the PE or N inhibition of PE along latitude were more significant in coniferous forests than in broadleaved forests (Fig. 3c). Specifically, the PE in coniferous forests increased with latitude, whereas N inhibition of PE decreased with latitude after controlling for the exogenous C quantity. The variation in the PE was mainly controlled by soil pH ($p < 0.05$; Fig. 3a), whereas the variation in N inhibition of PE was impacted by total N content in soil ($p < 0.05$; Fig. 3b).

4. Discussion

4.1. Geographic patterns of the PE

Our results revealed little dependence of the PE on latitude or MAT in the temperate forests in China (Fig. 2a), which was inconsistent with the findings at the global scale that a negative correlation between the PE and MAT was revealed. The thermal dependence of PE has been evidenced in previous studies (e.g., Bastida et al., 2019; Ren et al., 2021). For example, cold forests were reported to exhibit stronger PEs than temperate forests, followed by tropical forests (Bastida et al., 2019). However, the thermal limitation of microbial metabolism doesn't constrain PE critically in the studied temperate forests. Remarkably, pH-driven changes in soil environmental and microbial properties were demonstrated to mediate the geographic pattern of the PE in the temperate forests in China (Figs. 4 and 5). Mechanistically, soil pH regulates SOC mineralization through its impact on SOC solubility or by mediating microbial activity and function (Wang et al., 2017; Yang et al., 2021). The greatest PE is detected in the neutral pH condition as the activities of dominant microorganisms in soil were scarcely stressed (Aye et al., 2017; Blagodatskaya and Kuzyakov, 2008). Along the decreased pH gradient in acidic soils, microbial activity and decomposition processes were thus suppressed, weakening the degree of the PE (Feng et al., 2021; Yang et al., 2021). Furthermore, a significant correlation between the PE and MAT was detected at the global scale due to the broad range of thermal condition, which is also basically contributed to the regulation of soil pH (Fig. 3a). Therefore, soil acidification could be an important mechanism contributing to the decrease in the PE at the regional and global scales (Wang et al., 2016b).

As shaped by soil pH, variations in microbial community composition and relevant function were detected to directly mediate the degree of PE (Chen et al., 2014; Tian et al., 2019a; Tian et al., 2019b; Feng et al.,

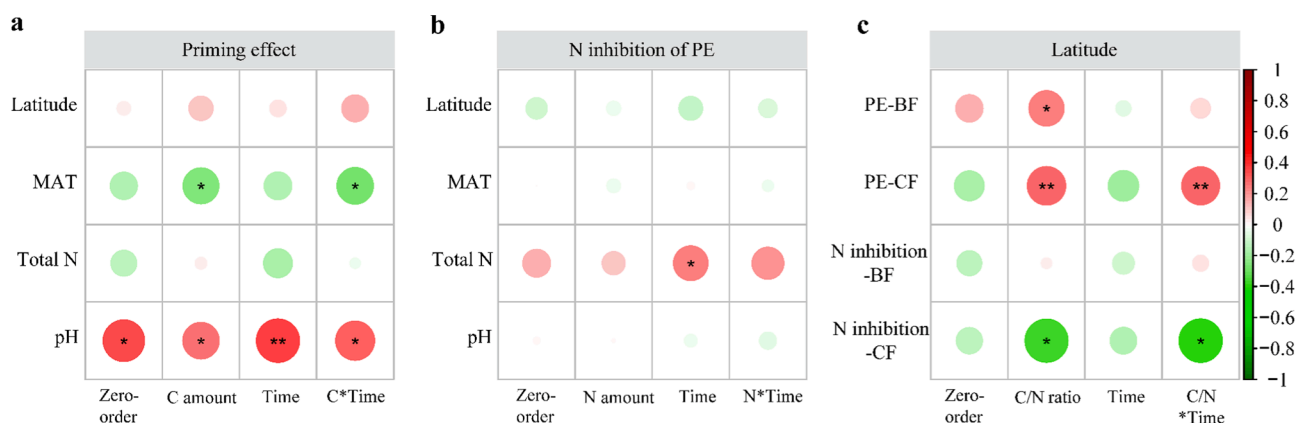


Fig. 3. Partial regressions between the priming effect (PE) and the latitude, MAT, and soil properties (a); between N inhibition of PE and the latitude, MAT, and soil properties (b); between latitude and the PE and N inhibition effect in broadleaved and coniferous forests (c). The size and color of the circles indicate the strength and sign of the correlation. Differences in circle size and color between the zero-order and controlled factors indicate the level of dependency of the correlation on the controlled variable. C/N amount and Time indicate the exogenous C/N quantity and experimental duration, respectively; PE-BF and PE-CF indicate the magnitude of priming effect in broadleaved and coniferous forests, respectively; N inhibition-BF and N inhibition-CF indicate the strength of N inhibition of PE in broadleaved and coniferous forests, respectively.

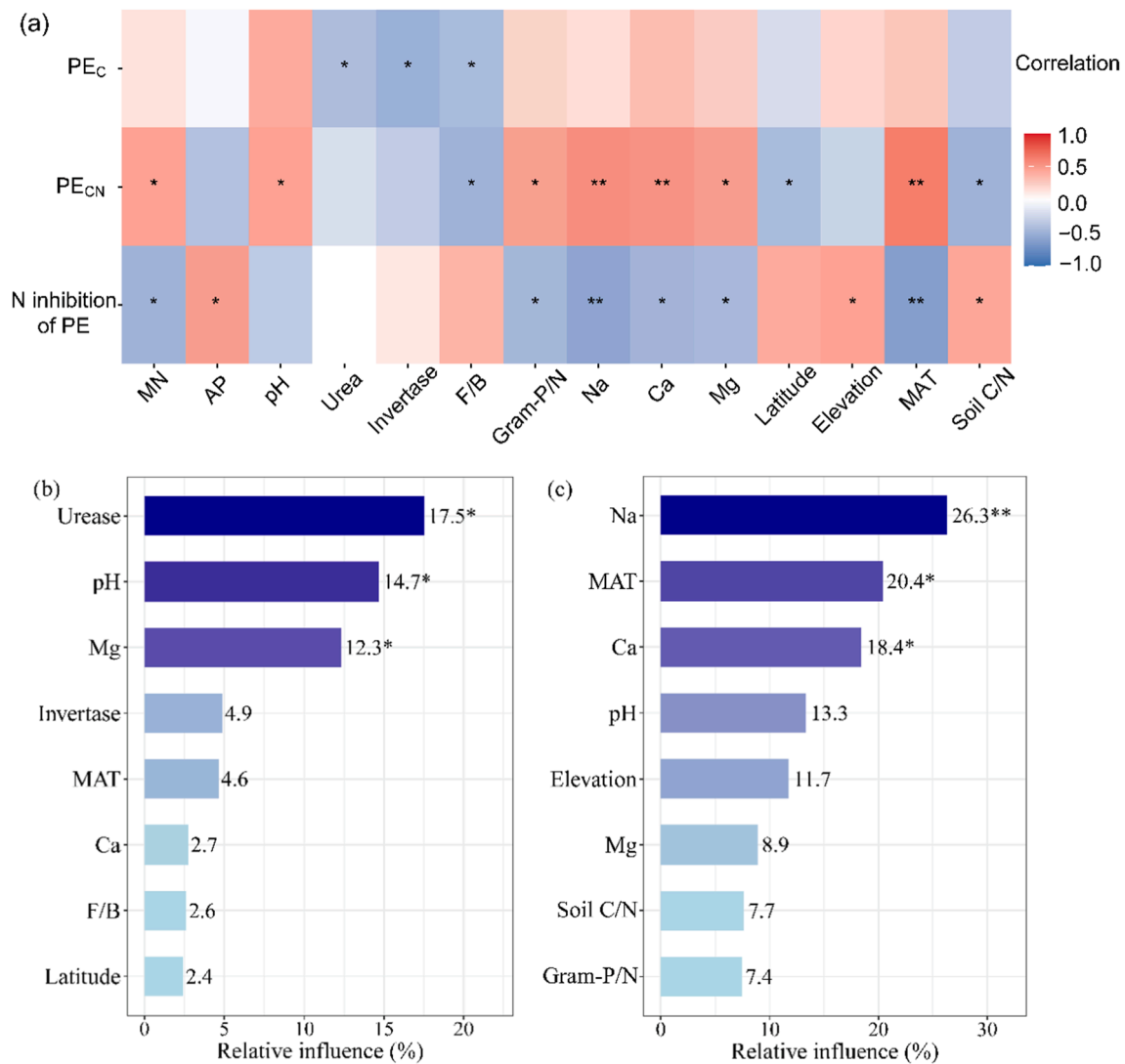


Fig. 4. Dependence of the priming effect (PE) and N inhibition of PE on environmental variables in temperate forests in China. Pearson correlations between the PE or N inhibition of PE and environmental variables (a); random forest analyses aiming to identify significant variables regulating the PE (b) and N inhibition of PE (c).

2021). The negative pathways through which fungal to bacterial PLFA ratio and urease activity impacting PE in the SEM highly confirmed this mechanism in temperate forests in China (Fig. 5a). Generally, bacteria (mainly r-strategists) respond faster to the glucose addition and win the short-term competition with fungi for labile C source, but have lower C-use efficiency (Chen et al., 2014). Fungi, in contrast, express a broader set of extracellular enzymes to break down recalcitrant compounds and are more efficient in C utilization (Fontaine et al., 2011). Consequently, less SOC would be decomposed following fresh C addition in soils with a high fungi to bacteria ratio to mine nutrients, especially N. Therefore, exogenous fresh C addition would not stimulate SOC decomposition in soil with abundant fungi as intensively as in fungi scarce soil, thus lessening the priming degree (Chen et al., 2014; Kuzyakov et al., 2000; Yin et al., 2016).

4.2. Geographic patterns of the N addition effect on PE

Consistent with our hypothesis, mineral N addition generally reduced the magnitude of the positive PE (Figs. 2 and S2), indicating that PE could be impacted by the imbalance between microbial demands for N and available N supply in soil (Chen et al., 2018; Fontaine et al., 2011; Wang et al., 2014). Adding mineral N along with C source would alleviate the dependence of microorganisms on released N via their

mining from soil organic matter, ultimately reducing the positive PE and hence benefitting SOC sequestration (Daly and Hernandez-Ramirez, 2020; Fontaine et al., 2011). This finding suggests the N mining theory to be a general mechanism regulating the response of the PE to N input in the absence of severe N limitation (Chen et al., 2014). Furthermore, N inhibition of PE was found to decrease with increasing MAT in temperate forests in China (Fig. 2d), thus anthropogenic N amendment in boreal and cold-temperate forests might be more efficient to sequester soil C by inhibiting the PE of SOC mineralization.

As indicated by the SEM, the MAT-dependence of N inhibition of PE was correlated with soil inherent N availability (Fig. 5b). Low N availability facilitate the microbial mining from soil organic matter for N, thus being more susceptible to exogenous N input (Fang et al., 2018; Feng et al., 2021; Nottingham et al., 2015; Su et al., 2022; Wang et al., 2014). Given that the N limitation became alleviated from cold to warm temperate forests as indicated by increasing mineral N contents in soils (Table 1), the response of microbial mining from SOC to exogenous N addition got impaired accordingly (Blagodatskaya and Kuzyakov, 2008; Feng and Zhu, 2021a). As a result, weaker inhibition effect of N addition on PE was detected in warm temperate forests with relatively low N-limitation (Fig. 2d and 4a). Across the globe, soil total N content was detected to positively associate with N inhibition of PE after controlling for experimental duration (Fig. 3b), contrasting the finding in our

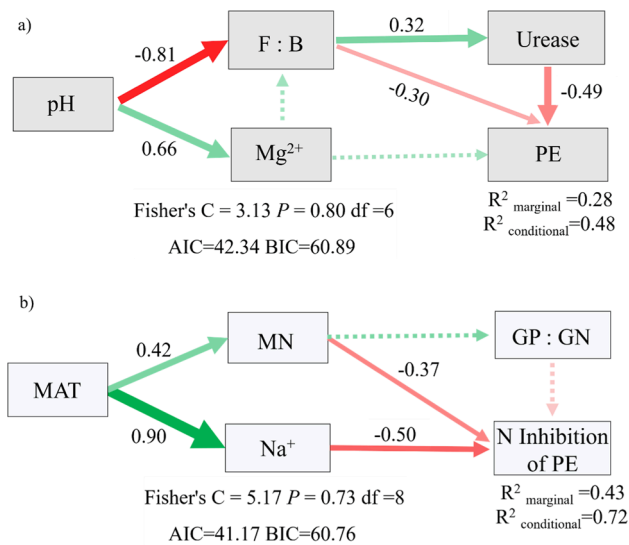


Fig. 5. Structural equation modeling (SEM) for geographic pattern of the priming effect (PE, a), and inhibition effect of N addition on PE (b) across nine temperate forests in this study. The numbers are standardized path coefficients, reflecting the importance of the variables within the model. F: B, the ratio of fungal to bacterial biomass; MN, mineral nitrogen content; Na^+ , exchangeable Na^+ content.

experiment. This is because N mining theory was challenged in some studies, where N amendment strengthened the PE apparently in N-deficient soils through a microbial stoichiometry decomposition process (Chen et al., 2014; Feng et al., 2021; Feng and Zhu, 2021a). This theory suggests that the concurrent additions of fresh C and N better match the microbial demand than sole C addition, thereby stimulating microbial activities and mineralization of SOM (Feng et al., 2021; Feng and Zhu, 2021a; Zhang et al., 2021). Additionally, differences in fresh C type as well as N deposition form from our incubation also contributed to the distinct finding, with complex fresh C like plant residue and organic N amendment being continuously reported to associate with positive N effects on PE (Tian et al., 2019a; Tian et al., 2019b; Zhang et al., 2021). Ultimately, the correlation between N inhibition of PE and MAT was not established across the globe, which might be masked by variations in culture temperature setting and forest types (Chen et al., 2018; Tian et al., 2019b; Wang et al., 2016a; Zhang et al., 2021).

The crucial role of exchangeable metal cations in mediating soil PE in response to N enrichment was emphasized in this study. Given that the N mining theory is suggested to be the dominant mechanism that controls the intensity of PE in response to N addition, microbial mining from SOC for N should be less weakened following N addition in soils with abundant exchangeable Na^+ (Fig. 5). Thus, it's reasonable to speculate that exchangeable metal cations benefit the mineralization of soil organic matter. Indeed, mineralization of soil organic matter is characterized by electron transfer, with organic matter serving as the electron donor (Chen et al., 2020). Thus, higher metal cations in soil might benefit the transport of electrons, accelerating the biochemical mineralization of SOC (Chen et al., 2020).

4.3. Impacts of forest type on the patterns of PE and N inhibition of PE

The PE in coniferous forests was more sensitive to latitudinal variation across the globe (Fig. 3a), which is in accordance with a meta-analysis of the PE in terrestrial ecosystems (Sun et al., 2019), thereby highlighting the effect of forest type in conjunction with latitude on soil C dynamics. In the collected observations, different distributions in soil pH between coniferous and broadleaved forests were found (Fig. S4), which might explain the greater sensitivity of PE to latitudinal variation in coniferous forests. As a primary stressor for soil C dynamics at the

global scale, soil pH controls substrate solubility and microbial activities, positively correlating with the PE in acid forest soils (Wang et al., 2017; Yang et al., 2021). Therefore, the broader gradient of soil acidity in coniferous forests across the globe (Fig. S4) determined a negative dependence of the PE on latitude. Correspondingly, the N inhibition of PE was significantly weakened with increasing latitude in coniferous other than broadleaved forests (Fig. 3c). As regulated by soil pH, the degree of microbial mining from SOC for N, i.e., the magnitude of PE gets stronger along the increased latitudinal gradient (Blagodatskaya and Kuzyakov, 2008; Feng and Zhu, 2021a). Accordingly, the response of microbial mining to exogenous N addition was amplified apparently in coniferous forests across the globe.

4.4. Limitations and implications for future study

Taking advantage of two complementary approaches, we explored the geographic patterns and controls of the PEs and their response to N addition. However, there may be some limitations that need to be illustrated. Firstly, we acknowledged that the results of N inhibition of PE presented in our study might be disputable. Indeed, we calculated the PE under N addition (PE_{CN}) by subtracting CO_2 concentration in un-amended control from SOC-derived CO_2 in glucose plus N addition treatment. However, increasing studies suggest that the treatment of sole N addition rather than unamended control should be treated as the reference to calculate the PE_{CN} , as N addition would probably impact the basal respiration of microorganisms (Feng and Zhu, 2021b). The direction and magnitude of N addition effects on PE generated by different calculations are different when N addition itself has impacted microbial decomposition of SOC (Feng and Zhu, 2021b). Therefore, this study lacked a control treatment, i.e., sole N addition, to more accurately estimate the effect of N application on PE. Full factorial experiments that include the treatment of sole N addition are recommended in future studies.

Actually, about half of the publications collected in this research contained the treatment of sole N addition. However, few of them calculated the magnitude of PE_{CN} treating sole N addition treatment as a reference, mainly showing an inhibition of PE by N application (e.g., Ehtesham and Bengtson, 2017; Tian et al., 2019a; Tian et al., 2019b; Wang et al., 2019). Therefore, although the terms of calculation methods in this study might be disputable, our finding didn't mislead the interpretation of the inhibition effect of N addition on PE.

Secondly, the determinants and underlying mechanisms of PE and its response to N addition at the global scale were not deeply explored. Our study combined a global meta-analysis with a regional experiment, but the variables taken advantage to evaluate the determinants were inco-ordinate in these two parts. Due to various experimental objectives, the environmental factors detected to interpret the PE or its response to N addition were different in the original case studies. Additionally, it is difficult to compare the importance of microbial traits in soil C dynamics among investigations because of the non-uniform classification of microbial groups and great uncertainties in enzyme and biomass measurements (Joergensen, 2022; Nannipieri et al., 2018). As a result, limited information of potential determinants could be derived from the meta-analysis, particularly with a lack of microbial mechanisms. We were thus only able to validate part of findings from the regional experiment on the global scale. Therefore, large-scale systematic investigations that provide unifying ecological context and an integrative approach are needed to understand their patterns and underlying mechanisms deeply.

5. Conclusions

By combining laboratory observations of nine temperate forests in China with a meta-analysis from global forests, discrepancy in the patterns of PE and N inhibition effect at various geographic scales was revealed. However, consistent controls were demonstrated at the

regional and global scales: with soil pH primarily controlling PE while N availability mediating N inhibition effect. Therefore, different observations may be obtained at different scales, emphasizing the importance of scale in studying spatial pattern. The “N mining theory” was proposed to be a general mechanism regulating the effect of N addition on PE over a broad geographic scale, thus N enrichment in soil to some extent benefits soil C sequestration. Greater sensitivity of the geographic patterns of PE and N inhibition effect in coniferous forests revealed the importance of introducing forest type in regulating the geographic patterns of terrestrial C dynamics. These findings on the geographic patterns and determinants of the PE and its response to N addition over broad scales provide precious information for accurately predicting C-climate feedbacks..

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

Acknowledgment

This research was supported by the National Natural Science Foundation of China (grant No. 31830015, 32171752, 32101334). We are very thankful to the editor and reviewers for their constructive comments and valuable suggestions on an earlier version of this manuscript.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.catena.2022.106806>.

References

- Aye, N.S., Butterly, C.R., Sale, P.W., Tang, C., 2017. Residue addition and liming history interactively enhance mineralization of native organic carbon in acid soils. *Biol. Fert. Soils* 53, 61–75. <https://doi.org/10.1007/s00374-016-1156-y>.
- Bastida, F., García, C., Fierer, N., Eldridge, D.J., Bowker, M.A., Abades, S., Alfaro, F.D., Asefaw Berhe, A., Cutler, N.A., Gallardo, A., García-Velázquez, L., Hart, S.C., Hayes, P.E., Hernández, T., Hseu, Z.Y., Jehmlich, N., Kirchmair, M., Lambers, H., Neuhauser, S., Peña-Ramírez, V.M., Pérez, C.A., Reed, S.C., Santos, F., Siebe, C., Sullivan, B.W., Trivedi, P., Vera, A., Williams, M.A., Luis Moreno, J., Delgado-Baquerizo, M., 2019. Global ecological predictors of the soil priming effect. *Nat. Commun.* 10, 3481. <https://doi.org/10.1038/s41467-019-11472-7>.
- Blagodatskaya, E., Kuzyakov, Y., 2008. Mechanisms of real and apparent priming effects and their dependence on soil microbial biomass and community structure: critical review. *Biol. Fert. Soils* 45, 115–131. <https://doi.org/10.1007/s00374-008-0334-y>.
- Bond-Lamberty, B., Thomson, A., 2010. Temperature-associated increases in the global soil respiration record. *Nature* 464, 579–582. <https://doi.org/10.1038/nature08930>.
- Chen, C., Hall, S.J., Coward, E., Thompson, A., 2020. Iron-mediated organic matter decomposition in humid soils can counteract protection. *Nat. Commun.* 11, 2255. <https://doi.org/10.1038/s41467-020-16071-5>.
- Chen, L., Liu, L., Mao, C., Qin, S., Wang, J., Liu, F., Blagodatsky, S., Yang, G., Zhang, Q., Zhang, D., Yu, J., Yang, Y., 2018. Nitrogen availability regulates topsoil carbon dynamics after permafrost thaw by altering microbial metabolic efficiency. *Nat. Commun.* 9, 3951. <https://doi.org/10.1038/s41467-018-06232-y>.
- Chen, R., Senbayram, M., Blagodatsky, S., Myachina, O., Dittert, K., Lin, X., Blagodatskaya, E., Kuzyakov, Y., 2014. Soil C and N availability determine the priming effect: microbial N mining and stoichiometric decomposition theories. *Glob. Chang. Biol.* 20, 2356–2367. <https://doi.org/10.1111/gcb.12475>.
- Daly, E.J., Hernandez-Ramirez, G., 2020. Sources and priming of soil N₂O and CO₂ production: nitrogen and simulated exudate additions. *Soil Biol. Biochem.* 149, 107942. <https://doi.org/10.1016/j.soilbio.2020.107942>.
- Davidson, A.L., Karl, R., Eric, P., Guy, J.D.K., 2016. Effects of soil type and composition of rhizodeposits on rhizosphere priming phenomena. *Soil Biol. Biochem.* 103, 512–521. <https://doi.org/10.1016/j.soilbio.2016.10.002>.
- Delgado-Baquerizo, M., Maestre, F.T., Reich, P.B., Trivedi, P., Osanai, Y., Liu, Y.R., Hamonts, K., Jeffries, T.C., Singh, B.K., 2016. Carbon content and climate variability drive global soil bacterial diversity patterns. *Ecol. Monogr.* 86, 373–390. <https://doi.org/10.1002/ecm.1216>.
- Di Lonardo, D.P., De Boer, W., Klein Gunnewiek, P.J.A., Hannula, S.E., Van der Wal, A., 2017. Priming of soil organic matter: Chemical structure of added compounds is more important than the energy content. *Soil Biol. Biochem.* 108, 41–54. <https://doi.org/10.1016/j.soilbio.2017.01.017>.
- Di Lonardo, D.P., Manrubia, M., De Boer, W., Zweepers, H., Veen, G.F., Van der Wal, A., 2018. Relationship between home-field advantage of litter decomposition and priming of soil organic matter. *Soil Biol. Biochem.* 126, 49–56. <https://doi.org/10.1016/j.soilbio.2018.07.025>.
- Ehtesham, E., Bengtson, P., 2017. Decoupling of soil carbon and nitrogen turnover partly explains increased net ecosystem production in response to nitrogen fertilization. *Sci. Rep.* 7, 10. <https://doi.org/10.1038/srep46286>.
- Fang, Y., Nazaries, L., Singh, B.K., Singh, B.P., 2018. Microbial mechanisms of carbon priming effects revealed during the interaction of crop residue and nutrient inputs in contrasting soils. *Glob. Chang. Biol.* 24, 2775–2790. <https://doi.org/10.1111/gcb.14154>.
- Feng, J., Tang, M., Zhu, B., 2021. Soil priming effect and its responses to nutrient addition along a tropical forest elevation gradient. *Glob. Chang. Biol.* 27, 2793–2806. <https://doi.org/10.1111/gcb.15587>.
- Feng, J., Zhu, B., 2021a. Global patterns and associated drivers of priming effect in response to nutrient addition. *Soil Biol. Biochem.* 153, 108118. <https://doi.org/10.1016/j.soilbio.2020.108118>.
- Feng, J., Zhu, B., 2021b. Does calculation method affect the nutrient-addition effect on priming? *Geoderma* 393, 115040. <https://doi.org/10.1016/j.geoderma.2021.115040>.
- Fontaine, S., Henault, C., Aamor, A., Bdioui, N., Bloor, J.M.G., Maire, V., Mary, B., Revallot, S., Maron, P.A., 2011. Fungi mediate long term sequestration of carbon and nitrogen in soil through their priming effect. *Soil Biol. Biochem.* 43, 86–96. <https://doi.org/10.1016/j.soilbio.2010.09.017>.
- Hartley, I.P., Hopkins, D.W., Sommerkorn, M., Wookey, P.A., 2010. The response of organic matter mineralisation to nutrient and substrate additions in sub-arctic soils. *Soil Biol. Biochem.* 42, 92–100. <https://doi.org/10.1016/j.soilbio.2009.10.004>.
- Joergensen, R.G., 2022. Phospholipid fatty acids in soil—drawbacks and future prospects. *Biol. Fert. Soils* 58, 1–6. <https://doi.org/10.1007/s00374-021-01613-w>.
- Kandeler, E., Gerber, H., 1988. Short-term assay of soil urease activity using colorimetric determination of ammonium. *Biol. Fert. Soils* 6, 68–72. <https://doi.org/10.1007/BF00257924>.
- Kuzyakov, Y., Friedel, J.K., Stahr, K., 2000. Review of mechanisms and quantification of priming effects. *Soil Biol. Biochem.* 32, 1485–1498. [https://doi.org/10.1016/S0038-0717\(00\)00084-5](https://doi.org/10.1016/S0038-0717(00)00084-5).
- Leff, J.W., Jones, S.E., Prober, S.M., Barberan, A., Borer, E.T., Firn, J.L., Harpole, W.S., Hobbie, S.E., Hofmockel, K.S., Knops, J.M., McCulley, R.L., La Pierre, K., Risch, A.C., Seabloom, E.W., Schutz, M., Steenbock, C., Stevens, C.J., Fierer, N., 2015. Consistent responses of soil microbial communities to elevated nutrient inputs in grasslands across the globe. *Proc. Natl. Acad. Sci. USA* 112, 10967–10972. <https://doi.org/10.1073/pnas.1508382112>.
- Liu, X.-J.-A., Finley, B.K., Mau, R.L., Schwartz, E., Dijkstra, P., Bowker, M.A., Hungate, B. A., 2020. The soil priming effect: Consistent across ecosystems, elusive mechanisms. *Soil Biol. Biochem.* 140, 107617. <https://doi.org/10.1016/j.soilbio.2019.107617>.
- Lu, R., 2000. *Soil and Agro-chemistry Analytical Methods*. China Agriculture Science and Technology Press, Beijing.
- Maestrini, B., Herrmann, A.M., Nannipieri, P., Schmidt, M.W.I., Abiven, S., 2014. Ryegrass-derived pyrogenic organic matter changes organic carbon and nitrogen mineralization in a temperate forest soil. *Soil Biol. Biochem.* 69, 291–301. <https://doi.org/10.1016/j.soilbio.2013.11.013>.
- Mason-Jones, K., Schmockel, N., Kuzyakov, Y., 2018. Contrasting effects of organic and mineral nitrogen challenge the N-Mining Hypothesis for soil organic matter priming. *Soil Biol. Biochem.* 124, 38–46. <https://doi.org/10.1016/j.soilbio.2018.05.024>.
- Meyer, N., Welp, G., Rodionov, A., Borchard, N., Martius, C., Amelung, W., 2018. Nitrogen and phosphorus supply controls soil organic carbon mineralization in tropical topsoil and subsoil. *Soil Biol. Biochem.* 119, 152–161. <https://doi.org/10.1016/j.soilbio.2018.01.024>.
- Murphy, C.J., Baggs, E.M., Morley, N., Wall, D.P., Paterson, E., 2015. Rhizosphere priming can promote mobilisation of N-rich compounds from soil organic matter. *Soil Biol. Biochem.* 81, 236–243. <https://doi.org/10.1016/j.soilbio.2014.11.027>.
- Nannipieri, P., Trasar-Cepeda, C., Dick, R.P., 2018. Soil enzyme activity: a brief history and biochemistry as a basis for appropriate interpretations and meta-analysis. *Biol. Fert. Soils* 54, 11–19. <https://doi.org/10.1007/s00374-017-1245-6>.
- Nottingham, A.T., Turner, B.L., Stott, A.W., Tanner, E.V.J., 2015. Nitrogen and phosphorus constrain labile and stable carbon turnover in lowland tropical forest soils. *Soil Biol. Biochem.* 80, 26–33. <https://doi.org/10.1016/j.soilbio.2014.09.012>.
- Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. *Science* 333, 988–993. <https://doi.org/10.1126/science.1201609>.
- Paterson, E., Sim, A., 2013. Soil-specific response functions of organic matter mineralization to the availability of labile carbon. *Glob. Chang. Biol.* 19, 1562–1571. <https://doi.org/10.1111/gcb.12140>.
- Perveen, N., Barot, S., Maire, V., Cotrufo, M.F., Shahzad, T., Blagodatskaya, E., Stewart, C.E., Ding, W., Siddiq, M.R., Dimassi, B., Mary, B., Fontaine, S., 2019. Universality of priming effect: An analysis using thirty five soils with contrasted properties sampled from five continents. *Soil Biol. Biochem.* 134, 162–171. <https://doi.org/10.1016/j.soilbio.2019.03.027>.

- R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rasmussen, C., Southard, R.J., Horwath, W.R., 2007. Soil mineralogy affects conifer forest soil carbon source utilization and microbial priming. *Soil Sci. Soc. Am. J.* 71, 1141–1150. <https://doi.org/10.2136/sssaj2006.0375>.
- Ren, C., Wang, J., Bastida, F., Delgado-Baquerizo, M., Yang, Y., Wang, J., Zhong, Z., Zhou, Z., Zhang, S., Guo, Y., Zhou, S., Wei, G., Han, X., Yang, G., Zhao, F., 2021. Microbial traits determine soil C emission in response to fresh carbon inputs in forests across biomes. *Glob. Chang. Biol.* 28, 1516–1528. <https://doi.org/10.1111/gcb.16004>.
- Rousk, J., Brookes, P.C., Baath, E., 2010. Investigating the mechanisms for the opposing pH relationships of fungal and bacterial growth in soil. *Soil Biol. Biochem.* 42, 926–934. <https://doi.org/10.1016/j.soilbio.2010.02.009>.
- Scharlemann, J.P., Tanner, E.V., Hiederer, R., Kapos, V., 2014. Global soil carbon: Understanding and managing the largest terrestrial carbon pool. *Carbon Manag.* 5, 81–91. <https://doi.org/10.4155/cmt.13.77>.
- Schinner, F., von Mersi, W., 1990. Xylanase-, CM-cellulase and invertase activity in soil: An improved method. *Soil Biol. Biochem.* 22, 511–515. [https://doi.org/10.1016/0038-0717\(90\)90187-5](https://doi.org/10.1016/0038-0717(90)90187-5).
- Su, J., Zhang, H., Han, X., Lv, R., Liu, L., Jiang, Y., Li, H., Kuzyakov, Y., Wei, C., 2022. 5300-Year-old soil carbon is less primed than young soil organic matter. *Glob. Chang. Biol.* 00, 1–16. <https://doi.org/10.1111/gcb.16463>.
- Sun, Z., Liu, S., Zhang, T., Zhao, X., Chen, S., Wang, Q., 2019. Priming of soil organic carbon decomposition induced by exogenous organic carbon input: a meta-analysis. *Plant Soil* 443, 463–471. <https://doi.org/10.1007/s11104-019-04240-5>.
- Tabatabai, M.A., 1982. Soil enzymes. In: Page, A.L., Miller, E.M., Keeney, D.R. (Eds.), *Methods of Soil Analysis, Part 2, Chemical and Microbiological Properties*. ASA, Madison, WI, pp. 903–947.
- Tian, P., Liu, S., Wang, Q., Sun, T., Blagodatskaya, E., 2019a. Organic N deposition favours soil C sequestration by decreasing priming effect. *Plant Soil* 445, 439–451. <https://doi.org/10.1007/s11104-019-04331-3>.
- Tian, P., Mason-Jones, K., Liu, S., Wang, Q., Sun, T., 2019b. Form of nitrogen deposition affects soil organic matter priming by glucose and cellulose. *Biol. Fert. Soils* 55, 383–391. <https://doi.org/10.1007/s00374-019-01357-8>.
- Tian, Q., Yang, X., Wang, X., Liao, C., Li, Q., Wang, M., Wu, Y., Liu, F., 2016. Microbial community mediated response of organic carbon mineralization to labile carbon and nitrogen addition in topsoil and subsoil. *Biogeochemistry* 128, 125–139. <https://doi.org/10.1007/s10533-016-0198-4>.
- Wang, Q., Chen, L., Yang, Q., Sun, T., Li, C., 2019. Different effects of single versus repeated additions of glucose on the soil organic carbon turnover in a temperate forest receiving long-term N addition. *Geoderma* 341, 59–67. <https://doi.org/10.1016/j.geoderma.2019.01.032>.
- Wang, Q., He, T., Liu, J., 2016a. Litter input decreased the response of soil organic matter decomposition to warming in two subtropical forest soils. *Sci. Rep.* 6, 33814. <https://doi.org/10.1038/srep33814>.
- Wang, Q., Liu, S., Tian, P., 2018. Carbon quality and soil microbial property control the latitudinal pattern in temperature sensitivity of soil microbial respiration across Chinese forest ecosystems. *Glob. Chang. Biol.* 24, 2841–2849. <https://doi.org/10.1111/gcb.14105>.
- Wang, X., Tang, C., Severi, J., Butterly, C.R., Baldock, J.A., 2016b. Rhizosphere priming effect on soil organic carbon decomposition under plant species differing in soil acidification and root exudation. *New Phytol.* 211, 864–873. <https://doi.org/10.1111/nph.13966>.
- Wang, Y., Wang, H., He, J., Feng, X., 2017. Iron-mediated soil carbon response to water-table decline in an alpine wetland. *Nat. Commun.* 8, 15972. <https://doi.org/10.1038/ncomms15972>.
- Wang, Q., Wang, S., He, T., Liu, L., Wu, J., 2014. Response of organic carbon mineralization and microbial community to leaf litter and nutrient additions in subtropical forest soils. *Soil Biol. Biochem.* 71, 13–20. <https://doi.org/10.1016/j.soilbio.2014.01.004>.
- Yang, F., Zhang, Z., Barberán, A., Yang, Y., Hu, S., Guo, H., 2021. Nitrogen-induced acidification plays a vital role driving ecosystem functions: Insights from a 6-year nitrogen enrichment experiment in a Tibetan alpine meadow. *Soil Biol. Biochem.* 153, 108107. <https://doi.org/10.1016/j.soilbio.2020.108107>.
- Yin, H., Phillips, R.P., Liang, R., Xu, Z., Liu, Q., 2016. Resource stoichiometry mediates soil C loss and nutrient transformations in forest soils. *Appl. Soil Ecol.* 108, 248–257. <https://doi.org/10.1016/j.apsoil.2016.09.001>.
- Zhang, Q., Cheng, L., Feng, J., Mei, K., Zeng, Q., Zhu, B., Chen, Y., 2021. Nitrogen addition stimulates priming effect in a subtropical forest soil. *Soil Biol. Biochem.* 160, 108339. <https://doi.org/10.1016/j.soilbio.2021.108339>.
- Zhang, X., Johnston, E.R., Barberán, A., Ren, Y., Lü, X., Han, X., 2017. Decreased plant productivity resulting from plant group removal experiment constrains soil microbial functional diversity. *Glob. Chang. Biol.* 23, 4318–4332. <https://doi.org/10.1111/gcb.13783>.
- Zhang, W., Wang, X., Wang, S., 2013. Addition of external organic carbon and native soil organic carbon decomposition: a meta-analysis. *PloS One* 8, e54779. <https://doi.org/10.1371/journal.pone.0054779>.