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Coupling and decoupling of soil carbon, nitrogen, phosphorus and potassium stocks along a 6 000-km northeast-southwest temperature gradient in China

Qiqi TAN[1,*], Yuzhen CHEN[2] and Guoan WANG[2,*]

[1] *College of Grassland Science and Technology, China Agricultural University, Beijing 100193 (China)*
[2] *College of Resources and Environmental Sciences, China Agricultural University, Beijing 100193 (China)*

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ABSTRACT

Soil nutrient stocks are crucial to ecosystem stability. Previous studies have examined variations in soil carbon (C), nitrogen (N), and phosphorus (P) stocks in response to climate warming; however, there is a lack of knowledge regarding how climate warming affects soil potassium (K) stock, although K is the second most abundant nutrient in plants. Furthermore, how climate warming affects the balance of soil C, N, P, and K stocks remains to be elucidated. Here, we investigated the changes in soil C, N, P, and K stocks under climate warming by sampling soils along a 6 000-km northeast-southwest temperature gradient in China. We found that soil C and N stocks significantly decreased with increasing temperature. Soil C and N stocks exhibited a stronger response to temperature than to soil properties (*i.e.*, soil pH and clay, silt, and sand contents), vegetation type, and soil type. However, soil P and K stocks remained stable with increasing temperature. Variations in soil P and K stocks were primarily regulated by soil properties, vegetation type, soil type, and soil parent material type. Furthermore, soil C stock was closely correlated with soil N stock along the temperature gradient, suggesting that coupled links between soil C and N stocks remained consistent across the temperature gradiet. The ratios of soil C and N stock to P and K stocks decreased with increasing temperature, indicating that soil C and N stocks declined more rapidly than soil P and K stocks under climate warming, thus resulting in the decoupling of C and N stocks from P and K stocks in the soil. Our findings revealed that soils might become more limited in C and N than in P and K under climate warming.

Key Words: climate warming, nutrient imbalance, soil fertility, soil nutrient stocks, soil nutrient stoichiometry

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INTRODUCTION

Air temperature across the world has risen in the past decades, and between 2030 and 2052, climate warming is predicted to reach 1.5 °C (IPCC, 2018). This threatens the maintenance of ecosystem stability. Soil nutrients significantly influence various ecosystem processes, including plant photosynthesis, microbial activity, and species composition, thereby playing a crucial role in the stability of terrestrial ecosystems (Sterner and Elser, 2002; Sardans *et al*., 2012). Soil nutrient stocks reflect the sustainability of soil nutrients (Li J W *et al*., 2022). Understanding the effect of climate warming on soil nutrient stocks is a high priority in global change research (Crowther *et al*., 2016; Poeplau, 2021; Soong *et al*., 2021). Previous research has primarily examined the variations in soil carbon (C), nitrogen (N), and phosphorus (P) stocks in response to climate warming. However, how soil potassium (K) stock responds to climate warming has been largely neglected (Sardans *et al*., 2006; Ylänne *et al*., 2020; McLaren and Buckeridge, 2021; Tan *et al*., 2021a; Yang *et al*., 2022). Potassium is the second most abundant nutrient in the photosynthetic tissues of plants and is regarded as a limiting nutrient for plant production, similar to N and P (Sardans and Peñuelas, 2015; Sardans *et al*., 2021). Studies investigating the change in soil K stock under climate warming will enhance our understanding of the effect of global warming on terrestrial ecosystems.

Artificial warming experiments and temperature-associated geographical pattern research are the two most commonly used methods for investigating the effect of warming on soil nutrient stocks (Tashi *et al*., 2016; Tang *et al*., 2018; Phillips *et al*., 2019; Ylänne *et al*., 2020; Kumar *et al*., 2021; McLaren and Buckeridge, 2021; Yang *et al*., 2022). The effect of warming on soil nutrient stocks could vary in experimental settings due to differences in the magnitude, duration, and method of warming (Chen *et al*., 2020). For example, experimental warming, resulting from the use of an open-top chamber, negatively affected soil labile C and N stocks (Xu *et al*., 2010). In contrast, a three-year free-air temperature enhancement experiment demonstrated that soil labile C and N pools increased as a result of experimental warming (Rui *et al*., 2011). Furthermore, information derived from artificial warming experiments is usually applicable

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*Corresponding author. E-mail: cautanqiqi@126.com, gawang@cau.edu.cn.

only for short periods (Melillo *et al*., 2011), while the effect of warming on soil nutrient dynamics generally lasts for a long time (Yuan *et al*., 2017). Soil research over a broad geographical scale across a temperature transect has been used to determine the effect of chronic warming on soil nutrient stocks (Sternberg and Yakir, 2015; Yuan *et al*., 2017; Wang *et al*., 2024). However, changes in precipitation may confuse the effect of temperature pattern on soil nutrient stocks, since temperature and precipitation are often collinearly correlated in natural environments (Post *et al*., 1982, 1985; Han *et al*., 2011; Hou *et al*., 2018). Considering that broad-scale field investigations cannot effectively isolate the effects of precipitation and temperature, one possible solution is to sample soil along an isohyet. Using this approach, we can detect the changes in soil nutrient stocks as temperature increases when precipitation variation is limited to a narrow range (Tan *et al*., 2020a).

The conserved internal associations of C, N, and P in organisms drive the coupled link between changes in C, N, and P in the soil (Finzi *et al*., 2011; Delgado-Baquerizo *et al*., 2013; Feng *et al*., 2019; Marañón-Jiménez *et al*., 2019; Han *et al*., 2023). Biological processes, such as vegetation growth and the mineralization of organic matter, mainly control soil C and N dynamics, whereas soil P variation is primarily regulated by geochemical processes like rock weathering and, to a lesser extent, is influenced by biological activities; for example, vegetation grown in wetter climate regimes accelerates rock weathering and brings P into the biosphere (Walker and Syers, 1976; Delgado-Baquerizo *et al*., 2013; Zhao, 2023). Hence, climate change may decouple soil C, N, and P changes, because biological and geochemical processes respond differently to climate change (Delgado-Baquerizo *et al*., 2013; Tan and Wang, 2016). For example, by analyzing the responses of soil nutrient stoichiometry to changing aridity at 224 dryland sites worldwide, Delgado-Baquerizo *et al*. (2013) observed that soil C and N contents first increased and then decreased with aridity, whereas soil P content increased with aridity. This led to decoupled variations in soil C, N, and P with changing aridity. Our previous study on the Qingzang Plateau of China also showed that increasing temperature reduced soil N stock but exerted no influence on soil P stock; therefore, soil N stock becomes decoupled from soil P stock under climate warming (Tan *et al*., 2021a). Apart from the coupling of C, N, and P in organisms, a coupled correlation between C-N-P and K in organisms also exists because organisms require various chemical elements to maintain their metabolism and complete their life cycle (Marschner, 2012; Tian *et al*., 2019; Ågren and Weih, 2020; Li Y G *et al*., 2022). Considering that soil K dynamic is mainly influenced by the weathering of rocks (Marschner, 2012; Tian *et al*., 2018; Srivastava *et al*., 2020), global warming may also cause the decoupling of soil C, N, and K stocks. This hypothesis stems from extending the current understanding of the effects of warming on soil C, N, and P stocks to include K as well. However, few studies have explored the variations in the coupled soil C, N, and K changes under climate warming.

To compensate for these knowledge gaps, we conducted a field investigation across a northeast-southwest transect along a 400-mm isohyet in China, with a temperature range of 14.2 °C. Our objectives were as follows: i) to elucidate the changes in soil C, N, P, and K stocks with changing temperature when precipitation variation was limited; ii) to examine the differences in soil C, N, P, and K stocks across different soil properties, vegetation types, and soil types; iii) to compare the contributions of temperature, soil properties, vegetation type, and soil type to soil C, N, P, and K changes; and iv) to confirm whether climate warming could break the coupled soil C, N, P, and K changes because biological and geochemical processes respond differently to increasing temperature. This study will deepen our knowledge of the long-term responses of soil C, N, P, and K stocks to climate warming and provide support for ecosystem management under climate warming.

MATERIALS AND METHODS

Site description

The northeast-southwest transect extended approximately 6 000-km and included 27 sampling sites (Table SI, see Supplementary Material for Table SI). It started from Site 1 (53°29′ N, 122°15′ E) in Northeast China to Site 27 (29°33′ N, 88°98′ E) in Southwest China. To ensure the reliability of climatic data, each sampling site was located near a meteorological station. The mean annual temperature (MAT) across the transect ranged from −5.1 to 9.1 °C, and the mean annual precipitation (MAP) varied from 355.9 to 451.6 mm. Both MAT and MAP represented the average values of more than 30 years. The sampling transect spanned eight vegetation types, six soil types, and four soil parent material types.

Soil sampling and chemical analysis

We completed soil sampling between July and August in 2013. The selected sampling area at each site was situated at a considerable distance from the city or town to eliminate the disturbance of human activity. We first chose a sampling area of 200 m^2 that was representative of local vegetation. The sampling sites we selected in the forest had a similar density of vegetation cover. Then, three 0.5 m × 0.5 m quadrats were randomly set in this area. Finally, we removed the O-horizon, including the litter layer, and used a volumetric soil ring (5 cm in height and 100 cm^3 in volume) to collect soil samples. Shen *et al*. (2001) analyzed soil ^{14}C apparent age at a depth of 5–10 cm, and found that it exceeded 100 years. Given that the obtained meteorological data represented changes in climate over recent decades, we collected surface soil samples from a depth of 0–5 cm. A total of 81 samples were collected. Because the formation time of the 0–5 cm soil at the sampling sites was less than 100 years, there might be no significant changes in climate, vegetation, and pedogenesis during this period. Thus, the effects of legacy climate, vegetation, and pedogenesis on soil nutrient stocks could be neglected.

Soil C and N contents were measured using an elemental analyzer (FlashEA 1112, CE Instruments, UK) (Tonks *et al.*, 2017). For soil P measurement, HNO_3-HF was first used to acidify soil samples, and then this mixture was digested using a microwave digestion system (MARS Xpress, CEM, USA), and an inductively coupled plasma optical emission spectrometer (ICP-OES) (ICP-OES 7300DV, PerkinElmer, USA) was finally used to analyze soil P content (Zhang *et al.*, 2018). The HF-$HClO_4$ flame photometric method was used to determine soil K content (Lu, 2000). A volumetric soil ring (5 cm in height and 100 cm^3 in volume) was used to obtain soil bulk density (BD) (Crovo *et al.*, 2021). The soil type at sampling sites 5–8 is classified as Chernozems, known for their shrinkage behavior. The BD of these soils could be affected by their wetness. Thus, we used pedotransfer functions to predict the soil BD at sampling sites 5–8 (Vervoort *et al.*, 2003, 2006; Han *et al.*, 2012; Wang *et al.*, 2014; Qiao *et al.*, 2019). Several pedotransfer functions have been developed to estimate soil C stock in China (Wu *et al.*, 2003; Song *et al.*, 2005; Yang *et al.*, 2007). Among these, Xu *et al.* (2015) showed that pedotransfer functions developed by Yang *et al.* (2007) had a lower root-mean-square error than those from Wu *et al.* (2003) and from Song *et al.* (2005); the dataset used in Yang *et al.* (2007) was also larger than those in Wu *et al.* (2003) and Song *et al.* (2005). Hence, the pedotransfer function ($\mathrm{BD} = 0.29 + 1.2033 \times \exp(-0.0775 \times \mathrm{SOM})$, where SOM is soil organic matter (%)) in Yang *et al.* (2007) was used to estimate the soil BD at sampling sites 5–8. We used a pH electrode to determine soil pH when the ratio of soil to water was 1:2.5 (Dick *et al.*, 2000). A particle size laser analyzer (Malvern Masterizer 2000, Malvern Instruments, UK) was used to measure the contents of soil clay, silt, and sand (Bittelli *et al.*, 2022). Soil C, N, P, and K stocks were calculated by multiplying soil C, N, P, and K contents by soil depth and BD.

Statistical analysis

Before conducting statistical analyses, soil C, N, P, and K stocks were ln-transformed to improve the normality of the data. Subsequently, we performed linear regression analyses to explore how soil C, N, P, and K stocks and the ratios of soil C and N stocks to P and K stocks changed along the temperature gradient. Correlation analyses of soil pH and clay, silt, and sand contents *vs*. soil C, N, P, and K stocks were conducted to detect how soil properties affected the variations in soil nutrient stocks. One-way analysis of variance (ANOVA) with least significant difference (LSD) multiple range tests was implemented to compare the differences in soil C, N, P, and K stocks among different vegetation types and soil types. To evaluate the contributions of MAT, MAP, soil properties, vegetation type, soil type, and soil parent material type to soil C, N, P, and K changes, we performed multiple regression analyses. In these analyses, vegetation type, soil type, and soil parent material type were introduced as dummy variables, as they are qualitative variables. All statistical analyses were conducted using SPSS 20.0 with a significance level of 0.05.

RESULTS

Changes in soil nutrient stocks with increasing temperature

Soil C, N, P, and K stocks ranged from 150.4 to 5 906.3, 15.1 to 318.4, 2.3 to 38.4, and 65.0 to 238.3 g m^{-2}, respectively, across the sampling transect (Table I). Soil C and N stocks showed a dramatic reduction, whereas soil P and K stocks showed no significant changes with increasing temperature (Fig. 1). A significant positive correlation was

TABLE I

Soil nutrient stocks (mean value) at the 0–5 cm depth from different sampling sites along a 6 000-km northeast-southwest temperature gradient in China

Site No.	Soil nutrient stock			
	C	N	P	K
	g m^{-2}			
1	4 274.6	202.9	21.0	82.5
2	3 776.0	285.2	25.4	99.6
3	2 884.6	184.7	24.4	222.2
4	1 915.5	144.2	30.2	146.7
5	959.1	57.5	8.0	142.0
6	410.1	18.3	2.3	67.8
7	501.2	49.6	15.4	167.9
8	878.3	80.6	22.2	163.9
9	533.6	35.1	16.0	82.2
10	484.6	35.1	25.1	130.9
11	182.5	19.2	22.6	71.6
12	258.2	16.0	19.1	106.1
13	150.4	15.1	8.4	71.4
14	1 031.1	98.2	25.5	152.6
15	2 961.5	246.7	22.8	173.5
16	783.5	62.1	38.4	197.0
17	2 614.6	234.3	24.6	238.3
18	1 299.9	70.5	24.7	165.7
19	697.8	51.0	31.0	209.7
20	2 732.0	216.4	25.4	103.3
21	1 913.5	126.2	18.2	135.1
22	5 906.3	318.4	27.3	169.0
23	1 941.5	116.8	8.8	76.8
24	614.9	77.6	25.4	93.8
25	362.1	69.4	23.7	80.5
26	2 315.2	176.2	26.2	92.7
27	382.3	60.8	19.8	65.0

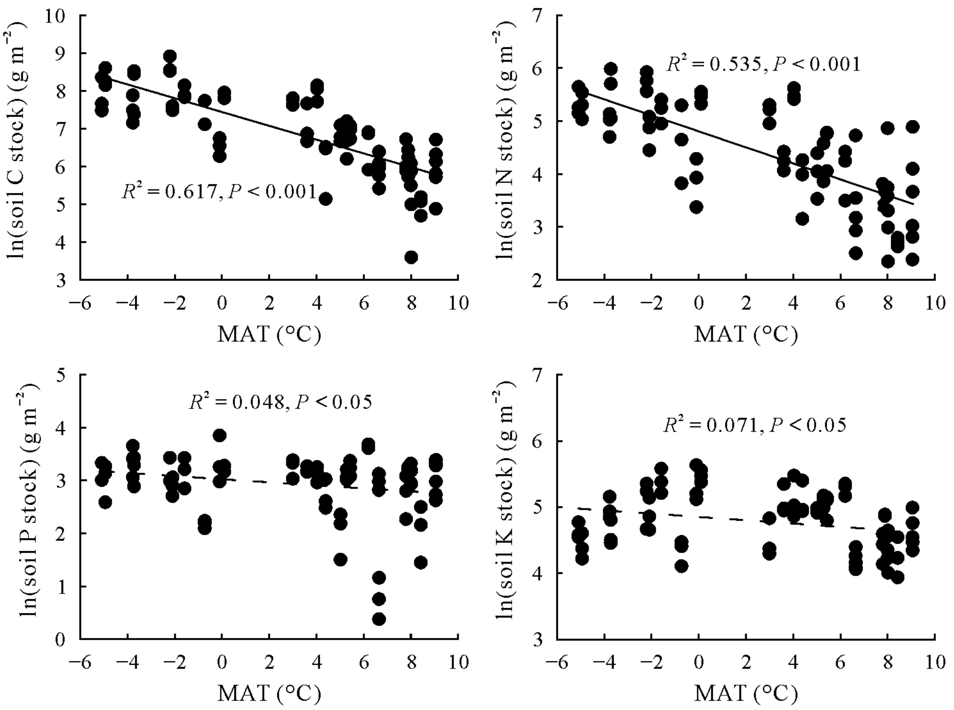

Fig. 1 Changes in soil nutrient stocks at the 0–5 cm depth with mean annual temperature (MAT) along a 6 000-km northeast-southwest temperature gradient in China.

observed between soil N and C stocks. (Fig. 2). The ratios of soil C and N stocks to P and K stocks significantly declined with increasing temperature (Fig. 3).

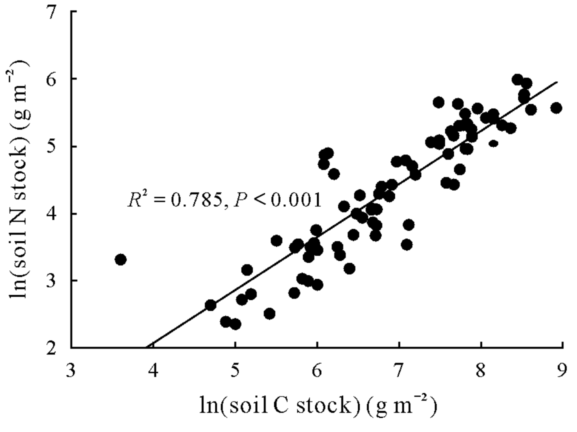

Fig. 2 Correlation between soil C and N stocks at the 0–5 cm depth along a 6 000-km northeast-southwest temperature gradient in China.

Correlations between soil nutrient stocks and soil properties, vegetation type and soil type

Soil C and N stocks declined with soil pH and sand content, whereas they increased with soil clay and silt contents (Fig. 4). Soil P stock did not vary with soil pH and clay content, but it increased with soil silt content and decreased with soil sand content. Soil K stock remained steady with soil pH, and it was positively correlated with soil clay and silt contents and negatively correlated with soil sand content.

Frigid temperate coniferous forests, temperate coniferous and broad-leaved mixed forests, and alpine meadows possessed the highest soil C and N stocks, followed by subalpine grasslands, alpine grasslands, temperate typical steppes, and temperate meadow steppes (Fig. 5). In contrast, semi-desert grasslands held the lowest soil C and N stocks. Soil P and K stocks in subalpine grasslands were higher than those found in the other vegetation types. However, semi-desert grasslands exhibited the lowest soil P and K stocks.

Umbrisols and Luvisols held the largest soil C and N stocks, followed by Cambisols, Leptosols, and Chernozems. Calcisols had the lowest soil C and N stocks (Fig. 6). Soil P and K stocks in Leptosols were higher than those in the other soil types.

Factors correlated with soil nutrient stocks

The MAT explained 61.7%, 53.5%, 4.8%, and 7.1% of the variations in soil C, N, P, and K stocks (Table II). When considering both MAT and MAP, 63.6%, 55.0%, 4.9%, and 13.9% of the variations in soil C, N, P, and K stocks were explained. With the inclusion of MAT, MAP, and soil properties, 73.0%, 63.1%, 30.5%, and 37.3% of the variations in soil C, N, P, and K stocks were explained. Moreover, 84.4%, 80.8%, 56.2%, and 66.4% of the variations in soil C, N, P, and K stocks were explained by MAT, MAP,

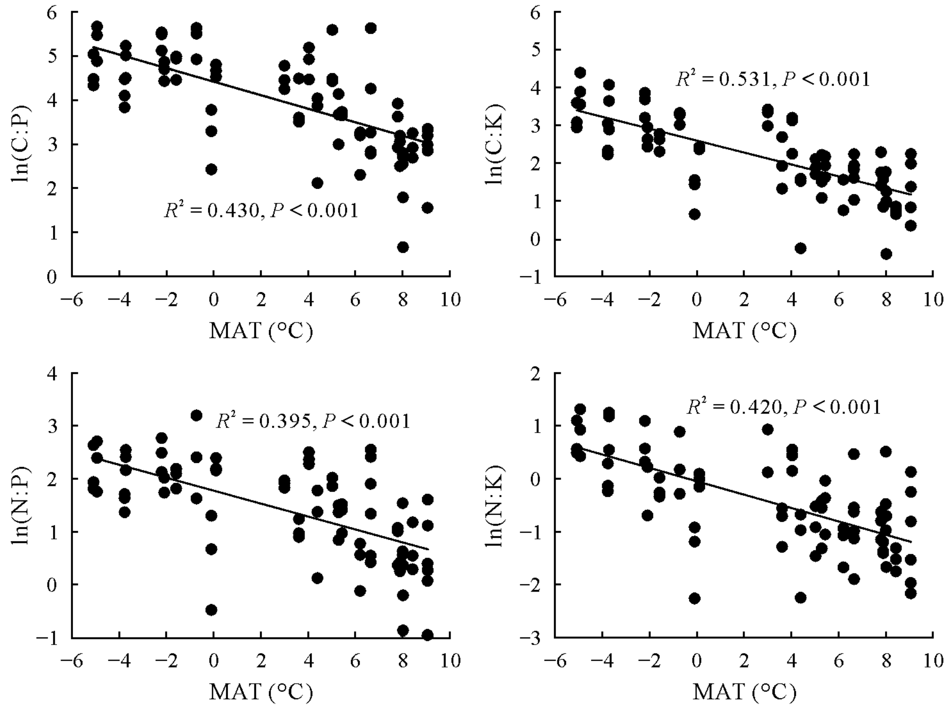

Fig. 3 Changes in ratios of soil C and N stocks to P and K stocks (C:P, C:K, N:P, and N:K) with mean annual temperature (MAT) along a 6 000-km northeast-southwest temperature gradient in China.

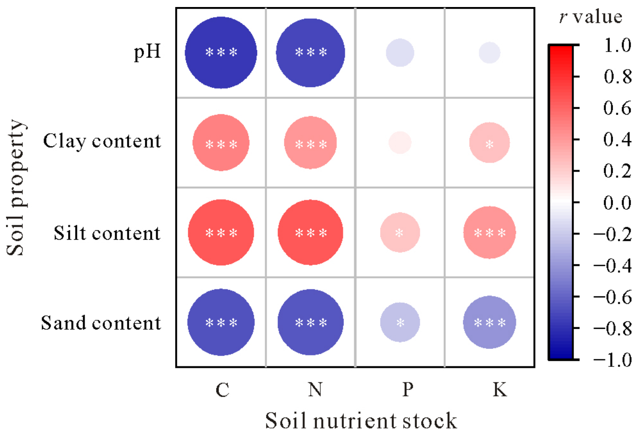

Fig. 4 Correlations between soil properties and nutrient stocks at the 0–5 cm depth along a 6 000-km northeast-southwest temperature gradient in China. Asterisks *, **, and *** indicate significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

soil properties, and vegetation type. Additionally, 81.6%, 80.1%, 53.8%, and 58.5% of the variations in soil C, N, P, and K stocks were explained by MAT, MAP, soil properties, and soil type. Finally, 75.4%, 71.0%, 61.0%, and 61.9% of the variations in soil C, N, P, and K stocks were explained by MAT, MAP, soil properties, and soil parent material type. These results indicated that MAT had a stronger control on soil C and N stocks than soil properties, vegetation type, and soil type. However, the changes in soil P and K stocks were mainly affected by soil properties, vegetation type, soil type, and soil parent material type.

DISCUSSION

Variations of soil C and N stocks along the temperature gradient and their drivers

Increasing temperature induced a dramatic reduction in soil C and N stocks (Fig. 1). This is consistent with previous studies examining the temperature patterns of soil C and N stocks across diverse geographical regions (Follett *et al.*, 2012; Tashi *et al.*, 2016; Tang *et al.*, 2018; Tan *et al.*, 2021a). For example, Follett *et al.* (2012) selected 14 sites, representing a broad range of climatic variables across the US Great Plains, and concluded that increasing temperature reduced soil C and N stocks. Tang *et al.* (2018) conducted an intensive field investigation, involving 14 371 sites across China, and observed that soil organic C density significantly decreased with increasing temperature. Our previous study, where soil samples were collected at MAT ranging from −5.1 to 9.1 °C on the Qingzang Plateau, found that soil N stock decreased along the temperature gradient (Tan *et al.*, 2021a). Moreover, by analyzing soil samples derived from a 16-year warming experiment, Phillips *et al.* (2019) reported that 16 years of artificial warming significantly reduced soil C and N stocks. Collectively, these findings indicate that global warming can negatively affect soil C and N stocks.

Mean annual temperature explained more than 50% of the variations in soil C and N stocks (Table II). Temperature changes could influence soil C stock through plant C input and microbial C mineralization. Increasing temperature not

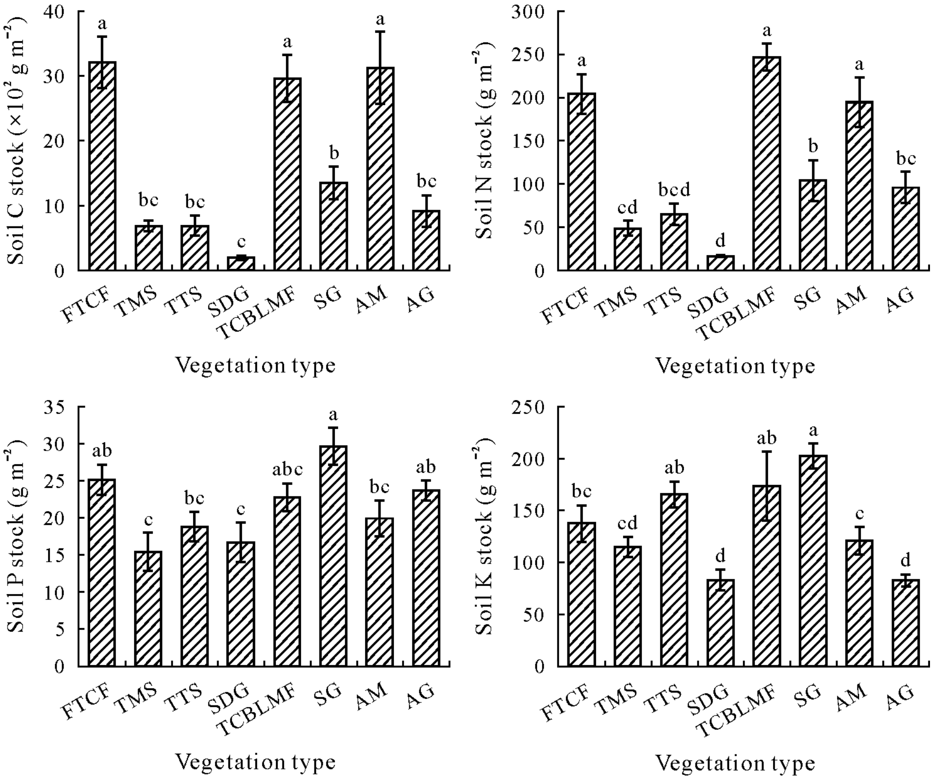

Fig. 5 Comparison of soil nutrient stocks at the 0–5 cm depth across different vegetation types along a 6 000-km northeast-southwest temperature gradient in China. Values are means with standard errors shown by vertical bars (n = 12, 15, 6, 9, 3, 12, 12, and 12 for frigid temperate coniferous forests (FTCF), temperate meadow steppes (TMS), temperate typical steppes (TTS), semi-desert grasslands (SDG), temperate coniferous and broad-leaved mixed forests (TCBLMF), subalpine grasslands (SG), alpine meadows (AM), and alpine grasslands (AG), respectively). Bars with different letters indicate significant differences among different vegetation types at $P < 0.05$.

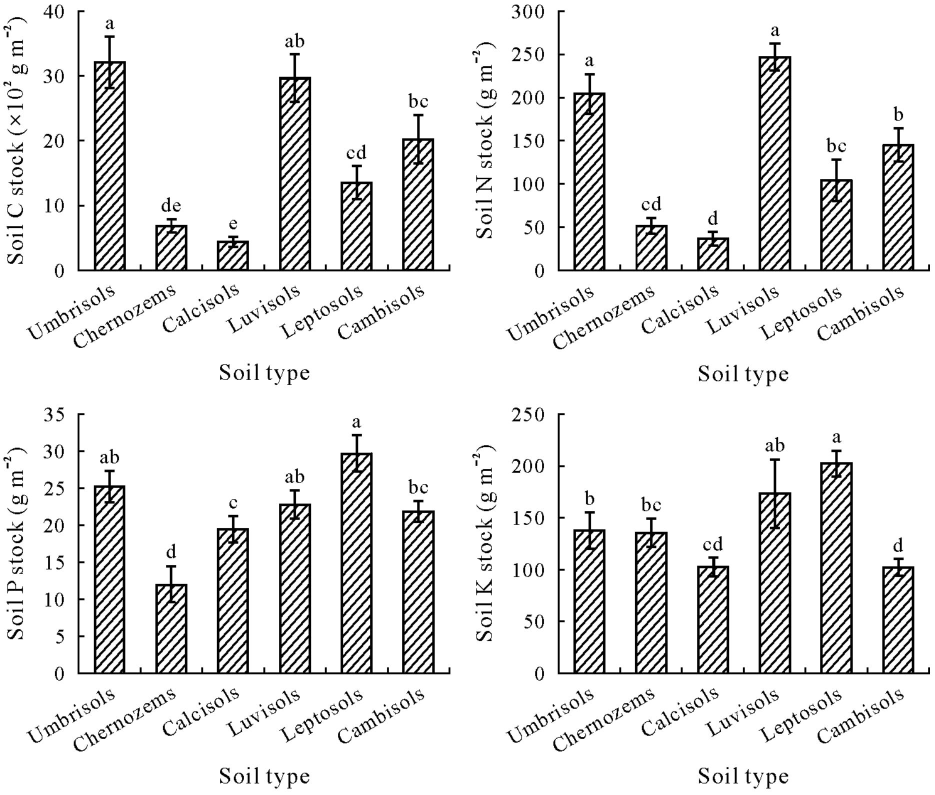

Fig. 6 Comparison of soil nutrient stocks at the 0–5 cm depth across different soil types along a 6 000-km northeast-southwest temperature gradient in China. Values are means with standard errors shown by vertical bars (n = 12, 12, 18, 3, 12, and 24 for Umbrisols, Chernozems, Calcisols, Luvisols, Leptosols, and Cambisols, respectively). Bars with different letters indicate significant differences among different soil types at $P < 0.05$.

TABLE II

Summaries of multiple regression analyses examining the relationships between soil nutrient stocks (0–5 cm) and variables such as mean annual temperature (MAT), mean annual precipitation (MAP), soil properties (SP, including pH and clay, silt, and sand contents), vegetation type (VT), soil type (ST), and parent material type (PM)

Explanatory variable included	R^2 value			
	Soil C stock	Soil N stock	Soil P stock	Soil K stock
MAT	0.617***	0.535***	0.048*	0.071*
MAT + MAP	0.636***	0.550***	0.049*	0.139**
MAT + MAP + SP	0.730***	0.631***	0.305***	0.373***
MAT + MAP + SP + VT	0.844***	0.808***	0.562***	0.664***
MAT + MAP + SP + ST	0.816***	0.801***	0.538***	0.585***
MAT + MAP + SP + PM	0.754***	0.710***	0.610***	0.619***

*, **, ***Significant at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

only enhanced plant growth but also promoted microbial decomposition (Tan *et al.*, 2020a). Given that our current soil sampling was carried out along the 400-mm isohyet, the limited water availability may further constrain plant production, as 400 mm is the threshold of an arid climate (Tang *et al.*, 2018). Thus, increasing temperature might exert a stronger influence on microbial C utilization than on plant C inputs, resulting in a reduction in soil C stock. Nitrogen in the soil is mainly sourced from the decomposition of soil organic matter (Tan *et al.*, 2021a). The reduction in soil C stock with increasing temperature could induce a negative impact of soil organic matter on soil N stock.

In addition to MAT, soil properties also influenced soil C and N stocks (Table II). Changes in soil C and N stocks were positively related to clay and silt contents, while they had a negative correlation with soil pH and sand content (Fig. 4). Previously, we found that soil pH increased along the temperature gradient (Tan *et al.*, 2021b). Microbial activity may be inhibited by alkaline soils, thereby exerting an additional negative influence on soil C and N stocks (Dendooven *et al.*, 2010). Soil clay and silt can absorb soil nutrients (De Rosa *et al.*, 2024); however, their contents decreased along the temperature gradient (Tan *et al.*, 2021b). Decreases in soil clay and silt contents have been reported to weaken the physical absorption and protection of soil nutrients (Wang *et al.*, 2020), and this may have further reduced soil C and N stocks under climate warming. Moreover, field capacity increases with soil clay content, which could affect vegetation growth and subsequently influence soil C and N stocks.

Changes in soil P and K stocks along the temperature gradient and their drivers

Soil P and K stocks remained steady with increasing temperature (Fig. 1). The present finding of the change in soil P stock with temperature is similar to that of our previous study conducted on the Qingzang Plateau, which demonstrated that increasing temperature did not influence or only slightly affected soil P dynamics (Tan *et al.*, 2021a). Kumar *et al.* (2021) investigated the effect of temperature on soil P stock by conducting samples along an altitudinal gradient in the Uttarakhand Himalayas and observed that soil P stock significantly declined with increasing temperature. Considering the strong correlation between temperature and precipitation across the altitudinal transect, the variation in soil P stock with temperature may have been influenced by the variation in precipitation. This may have resulted in the differences between our findings and those reported by Kumar *et al.* (2021). To the best of our knowledge, no previous study has explored the variation in soil K stock across a temperature transect. Here, we minimized variations in precipitation by sampling soils along the 400-mm isohyet and observed that soil K stock remained stable with increasing temperature (Fig. 1).

Soil properties strongly influenced soil P and K stocks (Table II). Soil clay and silt contents exerted a positive effect on soil P and K stocks, whereas soil sand content negatively influenced changes in soil P and K stocks (Fig. 4). Soil parent material and soil weathering regulate the variation in soil texture, consequently controlling soil P and K dynamics (Tian *et al.*, 2018; Wang *et al.*, 2020). Tian *et al.* (2018) examined the variations and controls of grassland soil nutrients across the Qingzang Plateau and found that soil texture primarily controlled soil P and K dynamics. We also observed that soil texture controlled soil P and K stocks (Fig. 4). Soil nutrients can be absorbed and protected by soil clay and silt; thus, soil P and K stocks increased with soil clay and silt contents. In addition, the soil sand content indicates the degree of rock weathering to some extent; soils with a greater sand content generally tend to exhibit a lower degree of rock weathering (Tan *et al.*, 2022). Hence, soil P and K stocks declined with increasing soil sand content.

Influences of vegetation type and soil type on soil nutrient stocks

Vegetation type significantly affected changes in soil C, N, P, and K stocks (Table II). Previous studies also observed the same findings that soil nutrient stocks were significantly influenced by the vegetation type (Chen *et al.*, 2018; Zhang *et al.*, 2021; Gogoi *et al.*, 2022). Frigid temperate coniferous forests and alpine meadows had the largest soil C and N stocks, while semi-desert grasslands had the smallest soil C and N stocks (Fig. 5). This could be attributed to the reason that frigid temperate coniferous forests and alpine meadows had the lowest MAT, whereas semi-desert grasslands had the highest MAT (Tan *et al.*, 2021b). Low temperatures can suppress the activity of microbes, resulting in the enrichment of soil C and N stocks. Similarly, Zhang *et al.* (2021) observed larger soil C and N stocks in coniferous forests and alpine meadows due to their higher altitudes and lower temperatures. However, this study also found that temperate coniferous and broad-leaved mixed forests had the highest soil C and N stocks (Fig. 5). This could be caused by the high clay and silt contents in temperate coniferous and broad-leaved mixed forests (Tan *et al.*, 2021b). Furthermore, different vegetation types can result in differences in plant root growth, plant aboveground productivity, and associated plant inputs (*e.g.*, litterfall and shallow rooting) (Jobbágy and Jackson, 2000). The potential effects of these processes on soil C and N stocks should be considered in future studies. Semi-desert grasslands retained the lowest soil P and K stocks (Fig. 5). Net primary production could be limited in the regions with a low rainfall regime (*i.e.*, semi-desert grasslands), and the movement of P and K from deeper roots in the soil profile to litterfall would be low, leading to less enrichment of P and K stocks in the topsoil (Zhao, 2023). Soil P and K stocks in subalpine grasslands were higher than those in the other vegetation types (Fig. 5). The relatively low MAT in the subalpine region indicated a higher rainfall regime in that area. This increased rainfall would facilitate the movement of P and K from deeper roots to the litterfall, resulting in the enrichment of soil P and K stocks.

Soil type also significantly affected soil C, N, P, and K stocks (Table II). Different soil types have different properties, influencing soil nutrient retention and loss (Tan *et al.*, 2021a). Umbrisols and Luvisols had higher soil C and N stocks compared to other soil types (Fig. 6). This was attributed to their higher clay and silt contents, which enhanced the nutrient absorption and thus led to the enrichment of soil C and N stocks (Tan *et al.*, 2021b). In contrast, Calcisols had the lowest soil C and N stocks (Fig. 6). Calcisols are widespread in arid and semi-arid environments, and their pedogenic development is slowed by recurrent drought periods, affecting essential soil-forming processes such as chemical weathering, organic matter accumulation, and clay translocation (Kalinin *et al.*, 2021; Kögel-Knabner and Amelung, 2021). Hence, Calcisols tend to have lower contents of soil clay and silt, resulting in reduced soil C and N stocks. Moreover, future studies should take into account the differences in vegetation growth and soil microbial activity across different soil types, as well as their effects on changes in soil C and N stocks. Soil P and K stocks in Leptosols were higher than those in the other soil types (Fig. 6). The Leptosol region possessed a lower MAT (Tan *et al.*, 2021b), resulting in a reduced absorption of P and K by plants. It also had a relatively low sand content in the soil (Tan *et al.*, 2021b), resulting from relatively high soil weathering. All of the above-mentioned processes contributed to the accumulation of soil P and K stocks in the Leptosols.

In addition to the influences of vegetation type and soil type on soil nutrient stocks, dust (loess) deposition usually varies across different sites, which could affect soil nutrient stocks (Eger *et al.*, 2013; Crowther *et al.*, 2019). However, the dust is mainly from the deserts and the Gobi region in western China, which has minimal organic matter and almost no naturally occurring minerals containing C and N. Thus, the effect of dust deposition on soil C and N stocks is very limited and may even be negligible. Phosphorus is mainly derived from apatite, which exists only in the form of phosphorite. The distribution of phosphorite in western China is concentrated in a few areas. Therefore, the influence of dust deposition on soil P stock may be negligible. Dust deposition may have an important effect on soil K stock, because many minerals such as potassium feldspar, black mica, and white mica contain K (Basak *et al.*, 2021). Li *et al.* (2008) reported that loess deposition became active during the dry conditions of the northwest winter monsoon. Active loess deposition may exert a stronger effect on the ratio of soil C stock to K stock than on the ratio of soil C stock to P stock. Ta *et al.* (2004) observed that the continuous deposition of loess could be composed more of silt-sized particles than sand-sized ones, leading to an increase in the silt content of loessial soils at a rate of 1.8–5 t ha^{-1} year^{-1}. It would affect soil texture and further influence soil C, N, P, and K stocks. Moreover, the temperature transect in this study spanned various types of soil parent materials (Table SI), which influenced soil P and K stocks (Table II). This influence arises from the fact that different rocks consist of different minerals, resulting in different elemental compositions. For example, Zheng *et al.* (1994) reported that intermediate weathered soils with a high mica content would have larger K reserves. In this study, soil clay and silt contents decreased along the temperature gradient, indicating that less plant-induced mineral weathering occurred as field conditions became drier (Tan *et al.*, 2022). Hence, investigating the P and K contents of topsoil-forming material would enhance our understanding of how the type of soil parent material influences soil P and K stocks.

Coupling and decoupling of soil C, N, P and K stocks under increasing temperature and their implications

Han *et al.* (2023) examined the variations in soil C and N dynamics with changing temperature and precipitation by sampling soils from the Tianshan Mountains, China. They reported that the coupled correlations between changes in soil C and N were maintained under climate change; soil C and N contents on sunny and shady slopes changed consistently across the altitude transect and showed a significant correlation with each other. In this study, we observed that both soil C and N stocks significantly reduced with increasing temperature (Fig. 1), and soil N stock showed a significant increase with the rise in soil C stock (Fig. 2). The consistent changes in soil C and N stocks and the strong correlation between these two stocks along the temperature gradient revealed coupled correlations between soil C and N under climate warming.

Coupled soil C, N, and P dynamics can be disrupted by rapid climate change (Delgado-Baquerizo *et al.*, 2013; Tan and Wang, 2016; Yu *et al.*, 2018). We observed that the ratios of soil C and N stocks to soil P stock decreased with increasing temperature (Fig. 3). This meant that soil C and N stocks declined more rapidly than soil P stock as temperature increased, resulting in the decoupling of soil C, N, and P stocks under climate warming. Similarly, the ratios of soil C and N stocks to K stock also decreased with increasing temperature (Fig. 3), suggesting that soil C and N stocks decreased more rapidly than soil K stock as temperature increased. Consequently, climate warming could break the coupled relationships among soil C, N, and K stocks. Changes in C and N levels in the soil are primarily regulated by biological processes, particularly the microbial utilization of soil organic matter (Delgado-Baquerizo *et al.*, 2013). Our study observed significant changes in soil C and N stocks with temperature, as fluctuations in temperature could affect microbial activity. However, soil P and K stocks did not respond to increasing temperature; instead, they were more strongly affected by soil properties than by temperature. Geochemical processes, particularly rock weathering, predominantly influence soil P and K dynamics (Tian *et al.*, 2018); as a result, soil properties have a stronger influence on soil P and K stocks. Owing to the diverse changes in biological and geochemical processes with increasing temperature, the changes in soil C and N stocks with temperature differed from those in soil P and K stocks (Fig. 1). Hence, we confirmed our hypothesis that climate warming could break the coupling of soil C, N, P, and K stocks.

Changes in soil C and N maintain various functions in terrestrial ecosystems and are crucial for soil-climate feedback mechanisms (Crowther *et al.*, 2016). This study identified coupled correlations between soil C and N stocks under the conditions of climate warming. These findings should be considered when modifying biogeochemical models that incorporate terrestrial C and N cycles. The rapid decreases in the ratios of soil C and N stocks to soil P and K stocks with increasing temperature indicated that climate warming could uncouple the equilibria between soil C and N stocks and soil P and K stocks. Our previous work conducted in the same sampling region showed that soil C and N contents decreased faster than soil P content as temperature increased (Tan *et al.*, 2021b). Taken together, these results suggested that climate warming could limit soil C and N to a greater extent than soil P and K. Moreover, the imbalance between soil C and N stocks and soil P and K stocks may further influence the stability of the stoichiometric ratios of C, N, P, and K in the soil. The availability of soil nutrients plays a crucial role in sequestering C into a more stable fraction within the soil C stock (Kirkby *et al.*, 2011, 2013, 2014). Thus, future studies should explore the effect of imbalanced soil nutrient stoichiometry on soil C sequestration and its interaction with vegetation type and soil type.

The Intergovernmental Panel on Climate Change predicted that climate warming could reach 1.5 °C between 2030 and 2052 and emphasized the importance of defending against the threat of climate warming (IPCC, 2018). Considering that effective ecosystem managements, such as plant mixture, forestation, and grazing exclusion, could promote soil C and N accumulation (Chen *et al.*, 2018; Fornara and Tilman, 2008; Li J W *et al.*, 2022; Xu *et al.*, 2023), these measures should be considered to address the potential shift in soil nutrient limitation resulting from climate warming. Furthermore, rising global temperatures are expected to alter the moisture-carrying capacity of monsoonal rains, increasing summer precipitation (Dong *et al.*, 2024). Changes in the precipitation regime could affect net primary production, thus influencing C and N fluxes in terrestrial ecosystems (Kannenberg *et al.*, 2024). Given that rainfall at all sampling sites mainly occurs in summer (Tan *et al.*, 2020b), the C and N limitation in the soil resulting from global warming could be further amplified, which should be considered in biogeochemical models containing terrestrial C and N cycles.

CONCLUSIONS

This study restricted precipitation to a narrow range by sampling soils along an isohyet, allowing for the analysis of changes in soil C, N, P, and K stocks in relation to temperature. We discovered that soil C and N stocks significantly decreased with increasing temperature, whereas soil P and K stocks remained unchanged. The effect of temperature on soil C and N stocks was stronger than that of soil properties, vegetation type, and soil type. Soil P and K stocks were mainly affected by soil properties, vegetation type, soil type, and soil parent material type. Soil C stock was closely correlated with soil N stock along the temperature gradient, suggesting the coupling of soil C and N stocks under climate warming. The ratios of soil C and N stocks to P and K stocks decreased with increasing temperature, revealing that soil C and N stocks responded more sensitively to climate warming compared to soil P and K stocks. This study highlights the coupling of soil C and N stocks and the decoupling of soil C and N stocks from soil P and K stocks under climate warming, while moisture maintained stable, providing a reference for ecosystem management in the context of climate warming.

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.

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SUPPLEMENTARY MATERIAL

Supplementary material for this article can be found in the online version.

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