

Scaling of Soil Carbon, Nitrogen, Phosphorus and C : N : P Ratio Patterns in Peatlands of China

ZHANG Zhongsheng, XUE Zhenshan, LYU Xianguo, TONG Shouzheng, JIANG Ming

(Key Laboratory of Wetland Ecology and Environment, Institute of Northeast Geography and Agroecology, Chinese Academy of Sciences, Changchun 130102, China)

Abstract: Inspired by the importance of Redfield-type C : N : P ratios in global soils, we looked for analogous patterns in peatlands and aimed at deciphering the potential affecting factors. By analyzing a suite of peatlands soil data ($n = 1031$), mean soil organic carbon (SOC), total nitrogen (TN) and total phosphorous (TP) contents were 50.51%, 1.45% and 0.13%, respectively, while average C : N, C : P and N : P ratios were 26.72, 1186.00 and 46.58, respectively. C : N ratios showed smaller variations across different vegetation coverage and had less spatial heterogeneity than C : P and N : P ratios. No consistent C : N : P ratio, though with a general value of 1245 : 47 : 1, was found for entire peatland soils in China. The Northeast China, Tibet, Zoigê Plateau and parts of Xinjiang had high soil SOC, TN, TP, and C : P ratio. Qinghai, parts of the lower reaches of the Yangtze River, and the coast zones have low TP and N : P ratio. Significant differences for SOC, TN, TP, C : N, C : P and N : P ratios were observed across groups categorized by predominant vegetation. Moisture, temperature and precipitation all closely related to SOC, TN, TP and their pairwise ratios. The hydrothermal coefficient (R_H), defined as annual average precipitation divided by temperature, positively and significantly related to C : N, C : P and N : P ratios, implying that ongoing climate change may prejudice peatlands as carbon sinks during the past 50 years in China.

Keywords: peatlands; C : N : P ratio; stoichiometry; climate change

Citation: Zhang Zhongsheng, Xue Zhenshan, Lyu Xianguo, Tong Shouzheng, Jiang Ming, 2017. Scaling of soil carbon, nitrogen, phosphorus and C : N : P ratio patterns in peatlands of China. *Chinese Geographical Science*, 27(4): 507–515. doi: 10.1007/s11769-017-0884-8

1 Introduction

According to the latest survey by China's State Forestry Administration during 2009–2013, China has $2.173\ 29 \times 10^7$ ha of natural marsh now, and peatlands occupy the expansive areas of wetlands in Northeast China, Zoigê Plateau, the Hengduan Mountains and the Qinghai Tibetan Plateau. Peatlands play an important role in the global carbon cycle, which is likely to be mediated through changes in climate, nutrients availability, vegetation conditions and microbe activities (Prentice and Fung, 1990; Dise *et al.*, 1993; Cramer *et al.*, 2001; Heimann and Reichstein, 2008). Global peatlands have

an estimated 609.9 Gt (1 Gt = 10⁹ g) C soil carbon pools (Page *et al.*, 2011), and boreal and subarctic peatlands comprise a carbon pool of 455 Pg that has accumulated during the postglacial period at an average net rate of 0.096 Pg/yr (1 Pg = 10¹⁵ g) (Gorham, 1991).

However, the fate of carbon in wetlands is to a major extent regulated by mass-balance principles and other key nutrient elements based on simple chemical reactions (Hessen *et al.*, 2004). Carbon (C), nitrogen (N) and phosphorus (P) are the three main biogenic elements and their interactions are carriers mediating mass and energy flow in ecosystems (Jablonska *et al.*, 2014). Thereby, deciphering C, N and P distribution patterns, C : N : P

Received date: 2016-07-04; accepted date: 2016-10-14

Foundation item: Under the auspices of National Key Research Program of China (No. 2016YFC0500404-5), National Natural Science Foundation of China (No. 41671081, 41471081, 41671087), Foundation of Jilin Province (No. 20140520141JH)

Corresponding author: XUE Zhenshan. E-mail: xuezhenshan@iga.ac.cn

© Science Press, Northeast Institute of Geography and Agroecology, CAS and Springer-Verlag Berlin Heidelberg 2017

stoichiometric characteristics and their influencing factors would contribute to understand links between ecological biogeochemistry and structures, processes and functions in peatlands.

All organisms, from cells to individuals, communities, ecosystems and even to the biosphere, require energy and nutritional resources in stoichiometric ratios, and so could be simplified and featured into some elementary ratios (Elser *et al.*, 2000; McGroddy *et al.*, 2004). C, N and P are the three main macro elements for biomass building, thus, the C : N : P ratio is important for deciphering relationships between organisms and environment medias. C : N : P ratios of organisms are species specific but trend to keep change in a narrow range owing to the consistent nitrogen and phosphorus contents in protein and nucleic acids, the two fundamental components of bodies (Elser *et al.*, 2000). Biogenic protein contains 16% nitrogen and nucleic acid has 9.5% phosphorus, which is independent with species (Loladze and Elser, 2011), so living beings could maintain stoichiometric homeostasis. About half of organic biomass is formed by carbon, and this ratio varies with species and cell types. In marine ecosystem, 'Redfield-ratio' infers an existence of well-constrained C : N : P ratio in plankton and water (Geider and La Roche, 2002). In contrast, our understanding of C, N and P relationships in terrestrial ecosystems is much less well developed (McGroddy *et al.*, 2004). On average, atomic C : N : P ratios in global soil (186 : 13 : 1) is well-constrained (Cleveland and Liptzin, 2007). But these ratios varied greatly from local to regional scales or among ecosystems (McGroddy *et al.*, 2004). It seems that C : N ratios could keep relatively steady within a narrow range, while C : P and N : P ratios varied violently, often closely depended on ecosystems.

Plants could adjust soil nutrients leading to a 'Redfield-type' ratio in forests (Yu *et al.*, 2011). C : N : P ratios of forest leaves and soil microbial biomass at the global scale are 1212 : 28 : 1 and 60 : 7 : 1, respectively (Cleveland and Liptzin, 2007). Average N : P ratio of world terrestrial plants is 12.7 (Agren, 2004). C : N : P ratio changes will impress main ecological processes by top-to-down or bottom-to-up. For example, mean C : P and N : P ratios in terrestrial plant leaves are both higher than those in their consumers, and plants restrict excessive consumers population by containing low P in their leaves (Agren, 2004). It seems that well-constrained

C : N : P ratio could be used as indicators testing ecosystem stability to a certain extent (Yu *et al.*, 2011).

Unlike that in the aquatic ecosystems, the relative immobility of the soil matrix tends to maintain spatial heterogeneity in element cycles, and nutrients are continuously redistributed by water, vegetation, soil fauna and parent materials (Hessen *et al.*, 2004). Diverse sets of C : N : P ratios have been proved in water, plankton, forest and grassland, however, little is available on C : N : P ratios in soil. One issue springs up in previous work is that persistence of stabilized C : N : P depends on research scales and ecosystems though it was identified to change in a narrow range on global scales (McGroddy *et al.*, 2004; Cleveland and Liptzin, 2007; Tian *et al.*, 2010). Moreover, soil stoichiometric features of carbon and nutrients on transition zone ecosystems like marshes and peatlands is still poorly constrained.

All beings are comprised of various elements gathering according to steady ratios restricted by simple chemical reactions in earth. It means that the biosphere can be reduced to simple ratios at different scales, from cells to individuals, communities and even to ecosystems (Michaels, 2003). In 1958, Redfield reported that molecule C : N : P ratios in marine planktons, 106 : 16 : 1 in consistent, well matched C : N : P ratio in seawater (Redfield, 1958). This well-constrained ratio, later named as Redfield Ratio, inspired ecologists to find whether similar ratios existed in other ecosystems. Previous work corroborated Redfield-like ratios in terrestrial ecosystems like grasslands, forest leaves and litter, micro biomass and global soils (McGroddy *et al.*, 2004; Cleveland and Liptzin, 2007; Mulder and Elser, 2009; Sardans *et al.*, 2012). Terrestrial organisms interact with the ambience and emulate themselves to environmental C : N : P ratios like soils. Could the steady C : N : P ratio in terrestrial organisms such as plant leaves, litters, and microbes induce consistent soil C : N : P ratios just like that found by Redfield in marine ecosystems (Redfield, 1958)? Though some previous works have made meaningful conclusions, no such works focus on peatlands.

Peatlands generally are a small sink for carbon dioxide, a large source of methane and a huge pool of organic carbon (Belyea and Malmer, 2004). Changes in nutrients budget are likely to have large effects on C fate in peatlands. Especially that human activities have changed natural nitrogen fluxes greatly (Vitousek *et al.*, 1997; Qu *et al.*, 2014), as nitrogen deposition increased

in most remote areas (Reay *et al.*, 2008), where peatlands were generally distributed. Nitrogen limitation to primary productivity and other biological processes is widespread in terrestrial ecosystems, especially in peatlands where nitrogen is inadequate, mainly comes from litter decomposition and partly from atmospheric deposition (Saunders and Kalff, 2001). Continuously increasing nitrogen deposition trends to greatly change C : N : P ratios in peatlands soils. However, C : N : P ratio distribution patterns and affecting factors are still poorly constrained. So, our objectives are: 1) to explore the general C, N, P and C : N : P ratios in China's peatland soils at a national scale; and 2) to decipher potential factors affecting C : N : P ratios. Based on these two objectives, we hope to promise for elucidation of inherent combined mechanisms of carbon and nutrients, and to demonstrate whether there is a well-constrained C : N : P ratio in China peatlands soils.

2 Materials and Methods

2.1 Peatland data sources

Geo-referenced peatland soil profiles were collected from the report of Peatland Resource Survey by the former Ministry of Geology and Mineral Resources of China in the 1980s and the *China Marsh* (Zhao, 1999). Totally, 1031 valid data series, and the properties investigated included geographical location, peatland areas, soil bulk density, predominant plant species, soil moisture, pH, soil organic matter (SOM), total nitrogen (TN), total phosphorus (TP), total sulfur (S), and humic acid and ash content, were involved in the present work (Fig. 1).

Soil organic carbon (SOC) was calculated as a portion of SOM which has been described by Wang *et al.* (2003). The mean C : N, C : P and N : P ratios were based on molecule basis. Considering that the peatland horizons are different for different sites, the 0–40 cm depth peat soils were selected to calculate the C : N : P ratios.

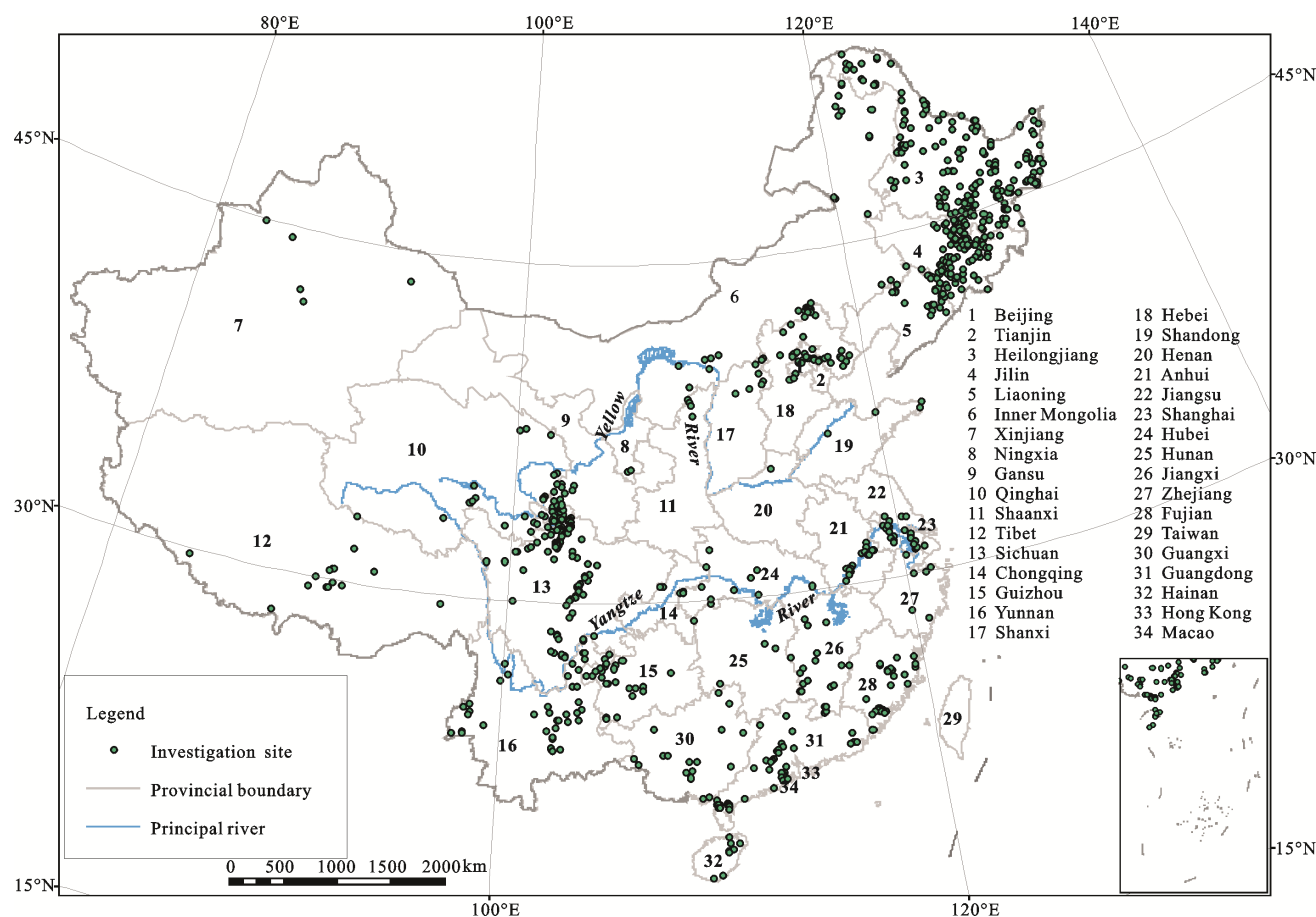


Fig. 1 Investigation sites of peatlands in China

2.2 Climate data sources

Climate information of 851 national meteorological stations during 1950–1990 of China was collected from the website <http://www.worldclim.org/current>. The Kriging interpolation by ArcGIS 9.2 software was used to get the corresponding longtime average annual mean temperature (T) and precipitation (Pre) in all peatland sites.

2.3 Statistical analysis

The SPSS 13.0 software (SPSS Inc., Chicago, Illinois) was employed for statistical analysis. The variance of analysis (ANOVA) with LSD (Least Square Difference) post hoc test of significance to compare SOC, TN, TP, C : N, C : P and N : P ratios within and across different groups. The mean values were reported with 95% confidence intervals.

3 Results

3.1 General patterns of soil SOC, TN, TP and C : N : P ratios in peatlands

Most peatlands are predominated by herbage, of which sedge, reed and wormwood are the most common and representative species. Pure moss communities are rare and often mixed with other flora such as *Carex*, *Phragmites* and *Xylophyta* (most are larches). Totally 1031 peatlands sites were categorized into four major groups by vegetation covers, herbage (labeled as H, $n = 899$), herbage and moss (labeled as H + M, $n = 22$), mixed communities including herbage, moss and woody plants (labeled as H + W + M, $n = 98$), and pure moss (labeled as M, $n = 12$). H, H + M, H + W + M and M groups were responsible for 87.2%, 2.1%, 9.5% and 1.2% of the total, respectively.

On the whole, mean SOC, TN and TP contents in China peatland soils were 50.51%, 1.45% and 0.13% respectively, while the average C : N, C : P and N : P ratios were 26.72, 1186.00 and 46.58, respectively

(Table 1). The frequency distribution analysis indicated that C : N, C : P and N : P ratios followed a skewed normal distribution pattern, with most C : N, C : P and N : P ratios in the range of 25–30, 500–2000, and 0–50, respectively (Fig. 2).

Statistically significant differences were proved by ANOVA analysis for SOC, TN, TP contents and their pairwise ratios among groups (SOC, $P < 0.001$; TN, $P < 0.001$; TP, $P < 0.001$), of which the highest SOC, TN and TP contents were found in M, H + M and H, respectively. Across-group significant differences were also tested for C : N, C : P and N : P ratios ($P < 0.001$). Much of this discrepancy owned to vegetation variation, which was partially or completely limited by nutrients changing during peatlands shifting to bogs from fens. When peatlands shifted to bogs from fens, dominant plant species converts to pure *Sphagnum* spp. from herbage or mixed communities. The highest C : N ratio in bogs showed the strongest N limitation while high C : P and N : P ratios implied the possible shortage of P supply.

3.2 Distribution patterns of SOC, TN, TP and C : N : P ratios

High SOC contents were found in the Northeast China and Southwest China, especially in the western Da Hinggan Mountains (46.38°N–50.18°N, 129.22°E–126.08°E), the Zoigê Plateau (32.93°N–34.32°N, 102.13°E–103.65°E) and the southern Tibet, while low SOC contents were observed in Inner Mongolia, Xinjiang, the North China Plain and the coastal regions of South China. TN contents varied in the range of 0.8%–2.0%, high in Northeast China, Xinjiang and the Zoigê Plateau and low in Qinghai, Hunan, Hubei, Fujian and Guangdong. TP contents were usually lower than 0.06%, high in Northeast China and Tibet, and low in Qinghai, the lower reaches of the Yangtze River and some coastal regions.

Table 1 Summary of C, N, P and C : N : P ratios in peatland soils of China

Category	SOC (%)	TN (%)	TP (%)	C : N	C : P	N : P	C : N : P
H	50.15±0.39	1.48±0.17	0.13±0.005	25.32±0.46	1050.00±42.00	44.61±1.67	1050:45:1
H+W+M	49.71±1.44	1.14±0.10	0.06±0.006	40.67±3.61	2545.00±307.00	67.60±8.06	2545:68:1
H+M	56.12±2.49	1.58±0.08	0.08±0.01	25.08±1.86	1475.00±188.00	63.45±7.13	1475:64:1
M	73.52±2.80	1.10±0.08	0.11±0.002	48.19±4.08	1914.00±613.00	35.87±9.48	1914:36:1
Overall	50.51±0.39	1.45±0.17	0.13±0.004	26.72±0.52	1186.00±47.00	46.58±1.62	1186:47:1

Notes: H, sites mainly covered by herbage; H+M, sites mainly covered by herbage and moss; H+W+M, sites mainly covered by mixed communities, including herbage, moss and woody plants; M, sites mainly covered by pure moss

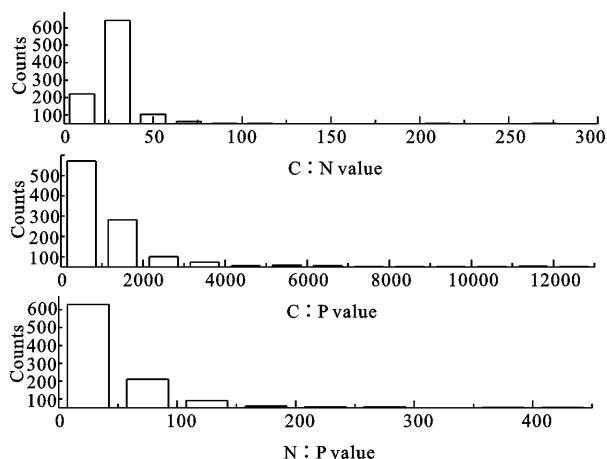


Fig. 2 Frequency distribution of C : N, C : P and N : P ratios

C : N ratios ranged from 15 to 35 with a few peaks and changed little spatially. In peatlands of Qinghai, Hunan, Hubei and southeast coastal regions, C : N ratios were generally lower than 10. Soil C : P ratios were spatially heterogeneous with the variance coefficient of 115%. Soil C : P ratios in most survey sites were higher than 1000, especially in zones around the Da Hinggan Mountain, middle Inner Mongolia, the Zoigê Plateau, Yunnan, and the lower reaches of the Yangtze River. Relatively low C : P ratios were detected in Tibet, Qinghai, Hebei, the northern Heilongjiang and Fujian Province.

Distribution patterns of soil N : P ratio, with the variance coefficient of 98%, were similar to C : P ratios. Soil N : P ratios in peatlands of Xinjiang, Tibet, Hebei, Hunan, Fujian and the northeast Heilongjiang Province were relatively low. Those sites in middle Inner Mongolia, Da Hinggan Mountain, Yunan, Guizhou and the lower reaches of the Yangtze River had high N : P ratios.

4 Discussion

4.1 Is there a Redfield-type ratio in peatlands soil of China?

Significant correlation coefficients between SOC and TN ($r_{CN} = 0.423$, $P < 0.0001$) and TP ($r_{CP} = -0.173$, $P < 0.001$) were detected. However, no significant correlations were found between N and P (r_{NP} , $P > 0.05$) in peat soils (Table 2). Based on reports of Tian *et al.* (2010) and Cleveland and Liptzin (2007), significant and pairwise correlations among C, N and P in soils necessitated the well-constrained C : N : P ratios. There was no Redfield-like C : N : P ratio in peatland

soils of China while the general soil C : N : P ratio was 1245 : 47 : 1, so there was no Redfield-type ratio.

Why there is no well-constrained C : N : P ratios in peatland soils as that in forest or grassland? Maybe difference between wetlands and forest or grassland could, at least partly, responsible for this contrast. Usually, forest or grassland are mature and stable ecosystems while wetlands, being located in the ecotones, are often susceptible to environmental factors like climate change and hydrological regimes variation (Erwin, 2009), and then shift to uplands or aquatics, which might induce the soil subjected to dramatic change and thereby cause unsteady C : N : P ratios.

Vegetation succession in peatlands from herbage to moss implies nutrient-rich fens shifting to oligotrophic bogs (Aerts *et al.*, 1999), as r_{CN} and r_{CP} were increasing when fens converted to bogs. High coefficients suggested more N limitation in fens and more P limitation in bogs, which might be ascribed to nutrients availabilities and leaf-level nutrient-use efficiency (Aerts *et al.*, 1999). Soil N or P in fens comes from multiple sources such as litter decomposition and exogenous input by water flows (Bai *et al.*, 2005). Nutrients in bogs mainly come from litter decomposition, leading to high correlation coefficients between C and nutrients than those in fens (Table 2).

4.2 Interactions of C : N, C : P and N : P ratios with nutrients (C, N, P, S)

Correlation analysis showed significant relationships between TP and r_{CN} , SOC and r_{NP} , S and r_{CP} , S and r_{NP} (Table 3). Globally or regionally, soil C : N ratios trend to fairly stable (Cleveland and Liptzin, 2007; Tian *et al.*, 2010), implying that other nutrients might have little influences on C : N ratios. However, the C : N ratio significantly and negatively related to TP contents in peatland soils, implying that P was one of the most important regulators for carbon and nitrogen circulation. In peatlands, litter decomposition incompletely relied on

Table 2 Correlation coefficients between C and nutrients in fens and bogs

Peatlands/Plant species	Taxa	r	P
Fens/Herbage	r_{CN}	0.549	<0.001
	r_{CP}	-0.128	<0.001
Bogs/Moss	r_{CN}	0.797	<0.001
	r_{CP}	-0.628	<0.05

Table 3 Correlation coefficients between C, N, P, S and C : N : P ratios

Taxa	<i>R</i>	<i>P</i>
C : N-TP	-0.113	<0.001
N : P-SOC	0.268	<0.001
C : P-S	0.352	<0.001
N : P-S	0.354	<0.001

microorganism activities and was restricted by anaerobic respiration strength due to high excessive moisture (Schimel *et al.*, 1999; Riutta *et al.*, 2012). Water-logged conditions yield carbon-rich soils and high C : N ratios in peatlands. Under poor-oxygen condition, massive triphosphadenine (ATP) were consumed by microbes to generate enough energy to finish anaerobic respiration (Chimner, 2004). As the key element of ATP, sufficiency P will form plenty of ATP, causing more strong decomposition and C : N decreasing finally.

Multiple-valence sulfate are proxies for soil oxidation and reduction condition. In wetlands soil, sulfates were the key and good electron acceptors due to oxygen shortage (Köpke *et al.*, 2005). On anaerobic conditions, sulfate reduction reactions at least partly, about 67% of the total, responsible for SOC mineralization (Finke *et al.*, 2007). So, sulfate might restrict carbon storage and sequestration in peatland soils. In addition, waterlogged situations induced large amounts of S²⁻, which would struggle for vacancies with soil organic matter as electron donors and concomitantly restrict soil organic carbon mineralization (Achnich *et al.*, 1995). In addition, S is one of the most important components of humic acid. Kirkby *et al.* (2011) reported that C : N : OP (organic P) : S ratios were constant for the stable portion of the soil organic material on the global scale, and S may be an important limiter for carbon storage and sequestration in terrestrial ecosystem.

4.3 Effects of environmental factors on SOC, TN, TP and C : N : P ratios

Wetlands are characterized by waterlogged soils and/or the presence of standing water during at least part of the year, unique soil conditions that differ from adjacent uplands, and the presence of vegetation adapted to wet conditions. Soil moisture in China peatlands was 72% on average. Significantly and positively correlations between moisture and SOC, TN, C : P and N : P ratios were observed while an opposite relation was found

between moisture and TP contents in soils (Table 4). Increasing moisture will hinder litter decomposition and lead to more C accumulation in peatland soils (Kayranli *et al.*, 2010). Unlike C and N, soil P mostly comes from weathering of the parent material. Soil P is further absorbed by plants and then released back to the surface by litter degradation in the organic form. High moisture contents, especially surface water, would yield much organic phosphorus, which flow out from wetlands and lead to P deficiency and C : P and N : P ratios rising.

Temperature and precipitation were identified as main factors affecting carbon and nutrients biogeochemical circulation in wetlands (Tarnocai, 2006). In the present work, mean annual temperature (*T*) and precipitation (*Pre*) significantly and negatively related to SOC, TN and TP in soils, while positively related to C : N, C : P and N : P ratios, respectively (Table 4). Correlations between *Pre* and SOC were not consistent with previous researches, which might due to peatlands spatial distribution rules in China. Many peatlands investigated are located in the subtropical and tropic zones, where precipitation is abundant or even excessive. However, peat here was not developed well and SOC accumulation rates were lower than those at northern high latitudes with less rainfall.

To reveal combined effects of climate change on C : N : P ratios, a hydrothermal coefficient (R_H) was defined. Considering that *T* in some sites was lower than 0°C, *T* was expressed as thermodynamic temperature when calculating R_H in order to avoid negative values. The formula was as the following:

$$R_H = \frac{Pre}{T + 273.15}$$

where *Pre* is the average annual precipitation (mm); *T* is the average annual temperature (K).

R_H negatively related to TP contents with the highest coefficient (Table 5). R_H in tropic zones was generally higher than those in temperate regions. Tropical ecosys-

Table 4 Correlation coefficients between environmental factors and SOC, TN, TP and C : N : P ratios

Taxa	SOC	TN	TP	C : N	C : P	N : P
Moisture	0.407**	0.294**	-0.116**	0.004	0.193**	0.215**
Temperature	-0.150**	-0.155**	-0.199**	0.244**	0.394**	0.352**
Precipitation	-0.095**	-0.117**	-0.255**	0.289**	0.414**	0.344**

Note: ***P* < 0.01

Table 5 Correlation coefficients between R_H and SOC, TN and TP contents

Taxa	R	P
R_H vs. SOC	-0.088	<0.001
R_H vs. TN	-0.111	<0.001
R_H vs. TP	-0.257	<0.001

tems are P-limited due to older soil age (Vitousek *et al.*, 2010). Thus, P might be not the limitation in peatlands.

R_H positively and significantly related to C : N, C : P and N : P ratios (Fig. 3). Precipitation increasing or temperature reducing will lead to R_H rising. During the past 50 years, temperature in China has increased greatly at the rate of 0.22°C/10yr, while precipitation little changed (Ren *et al.*, 2005). In Northeast China, climate was characterized by warming and drying trend (Song *et al.*, 2012), and R_H was decreasing in consequence with soil C : N, C : P and N : P ratios reduction, giving us some enlightenments that climate may reduce the nutrient limitation in peatlands and would prejudice functions of peatlands as carbon sinks.

5 Conclusions

In conclusion, C : N ratios showed smaller variations across different vegetation coverage and had less spatial heterogeneity than C : P and N : P ratios. No consistent C : N : P ratio, though with a general value of 1245 : 47 : 1, was found for entire peatland soils in China. Moisture, temperature and precipitation all closely related to SOC, TN, TP and their pairwise ratios.

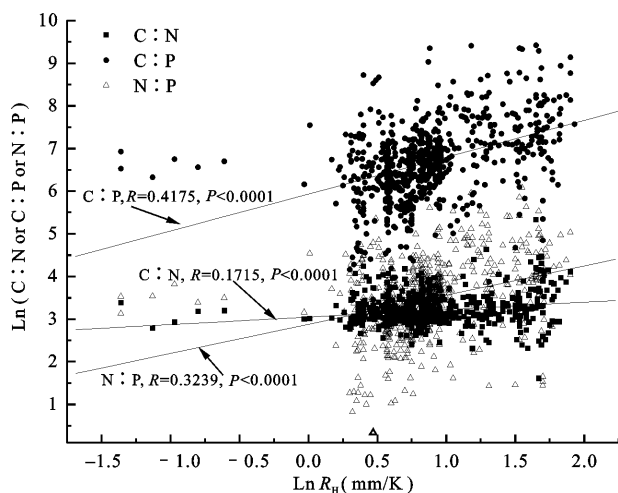


Fig. 3 Relationships between R_H and C : N, C : P and N : P ratios

The hydrothermal coefficient, defined as annual average precipitation divided by temperature, positively and significantly related to C : N, C : P and N : P ratios, implying that ongoing climate change may prejudice peatlands as carbon sinks during the past 50 years in China.

References

- Achtnich C, Bak F, Conrad R, 1995. Competition for electron donors among nitrate reducers, ferric iron reducers, sulfate reducers, and methanogens in anoxic paddy soil. *Biology and Fertility of Soils*, 19(1): 65–72. doi: 10.1007/BF00336349.
- Aerts R, Verhoeven J T A, Whigham D F, 1999. Plant-mediated controls on nutrient cycling in temperate fens and bogs. *Ecology*, 80(7): 2070–2181. doi: 10.1890/0012-9658(1999)080[2170:PMCONC]2.0.CO;2
- Agren G I, 2004. The C : N : P stoichiometry of autotrophs—Theory and observations. *Ecology Letters*, 7(3): 185–191. doi: 10.1111/j.1461-0248.2004.00567.x
- Bai Junhong, Ouyang Hua, Deng Wei *et al.*, 2005. A review on nitrogen transmission processes in natural wetlands. *Acta Ecologica Sinica*, 25(2): 326–333. (in Chinese)
- Belyea L R, Malmer N, 2004. Carbon sequestration in peatland: patterns and mechanisms of response to climate change. *Global Change Biology*, 10(7): 1043–1052. doi: 10.1111/j.1529-8817.2003.00783.x
- Chimner R A, 2004. Soil respiration rates of tropical peatlands in Micronesia and Hawaii. *Wetlands*, 24(1): 51–56. doi: 10.1672/0277-5212(2004)024[0051:SRROTP]2.0.CO;2
- Cleveland C C, Liptzin D, 2007. C : N : P stoichiometry in soil: is there a ‘Redfield ratio’ for the microbial biomass? *Biogeochemistry*, 85(3): 235–252. doi: 10.1007/s10533-007-9132-0
- Cramer W, Bondeau A, Woodward F I *et al.*, 2001. Global response of terrestrial ecosystem structure and function to CO₂ and climate change: results from six dynamic global vegetation models. *Global Change Biology*, 7(4): 357–373. doi: 10.1046/j.1365-2486.2001.00383.x
- Dise N B, Gorham E, Verry E S, 1993. Environmental-factors controlling methane emissions from peatlands in Northern Minnesota. *Journal of Geophysical Research-Atmospheres*, 98(D6): 10583–10594. doi: 10.1029/93JD00160
- Elser J J, Fagan W F, Denno R F *et al.*, 2000. Nutritional constraints in terrestrial and freshwater food webs. *Nature*, 408(6812): 578–580. doi: 10.1038/35046058
- Erwin K L, 2009. Wetlands and global climate change: the role of wetland restoration in a changing world. *Wetlands Ecology and Management*, 17(1): 71–84. doi: 10.1007/s11273-008-9119-1
- Finke N, Vandieken V, Jorgensen B B, 2007. Acetate, lactate, propionate, and isobutyrate as electron donors for iron and sulfate reduction in Arctic marine sediments, Svalbard. *FEMS*

- Microbiology Ecology*, 59(1): 10–22. doi: 10.1111/j.1574-6941.2006.00214.x
- Geider R J, Roche J, 2002. Redfield revisited: variability of C:N:P in marine microalgae and its biochemical basis. *European Journal of Phycology*, 37(1): 1–17. doi: 10.1017/S0967026201003456
- Gorham E, 1991. Northern peatlands: Role in the carbon-cycle and probable response to climatic warming. *Ecological Applications*, 1(2): 182–195. doi: 10.2307/1941811
- Heimann M, Reichstein M, 2008. Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature*, 451(7176): 289–292. doi: 10.1038/nature06591
- Hessen D O, Agren G I, Anderson T R *et al.*, 2004. Carbon, sequestration in ecosystems: The role of stoichiometry. *Ecology*, 85(5): 1179–1192. doi: 10.1890/02-0251
- Jablonska E, Falkowski T, Chormanski J *et al.*, 2014. Understanding the long term ecosystem stability of a fen mire by analyzing subsurface geology, eco-hydrology and nutrient stoichiometry—case study of the Rospuda Valley (NE Poland). *Wetlands*, 34(4): 815–828. doi: 10.1007/s13157-014-0544-z
- Köpke B, Wilms R, Engelen B *et al.*, 2005. Microbial diversity in coastal subsurface sediments: a cultivation approach using various electron acceptors and substrate gradients. *Applied and Environmental Microbiology*, 71(12): 7819–7830. doi: 10.1128/AEM.71.12.7819-7830.2005
- Kayranli B, Scholz M, Mustafa A *et al.*, 2010. Carbon storage and fluxes within freshwater wetlands: a critical review. *Wetlands*, 30(1): 111–124. doi: 10.1007/s13157-009-0003-4
- Kirkby C A, Kirkegaard J A, Richardson A E *et al.*, 2011. Stable soil organic matter: a comparison of C : N : P : S ratios in Australian and other world soils. *Geoderma*, 163(3–4): 197–208. doi: 10.1016/j.geoderma.2011.04.010
- Loladze I, Elser J J, 2011. The origins of the Redfield nitrogen-to-phosphorus ratio are in a homeostatic protein-to-rRNA ratio. *Ecology Letters*, 14(3): 244–250. doi: 10.1111/j.1461-0248.2010.01577.x
- McGroddy M E, Daufresne T, Hedin L O, 2004. Scaling of C : N : P stoichiometry in forests worldwide: implications of terrestrial Redfield-type ratios. *Ecology*, 85(9): 2390–2401. doi: 10.1890/03-0351
- Michaels A F, 2003. The ratios of life. *Science*, 300(5621): 906–907. doi: 10.1126/science.1083140
- Mulder C, Elser J J, 2009. Soil acidity, ecological stoichiometry and allometric scaling in grassland food webs. *Global Change Biology*, 15(11): 2730–2738. doi: 10.1111/j.1365-2486.2009.01899.x
- Page S E, Riele J O, Banks C J, 2011. Global and regional importance of the tropical peatland carbon pool. *Global Change Biology*, 17(2): 798–818. doi: 10.1111/j.1365-2486.2010.02279.x
- Prentice K C, Fung I Y, 1990. The sensitivity of terrestrial carbon storage to climate change. *Nature*, (6279)346: 48–51. doi: 10.1038/346048a0
- Qu F, Yu J, Du S *et al.*, 2014. Influences of anthropogenic cultivation on C, N and P stoichiometry of reed-dominated coastal wetlands in the Yellow River Delta. *Geoderma*, 235–236(4): 227–232. doi: 10.1016/j.geoderma.2014.07.009
- Reay D S, Dentener F, Smith P *et al.*, 2008. Global nitrogen deposition and carbon sinks. *Nature Geoscience*, 1(7): 430–437. doi: 10.1038/ngeo230
- Redfield A C, 1958. The biological control of chemical factors in the environment. *American Scientist*, 46(3): 205–221.
- Ren Guoyu, Guo Jun, Xu Mingzhi *et al.*, 2005. Climate change of China's mainland over past half century. *Acta Meteorologica Sinica*, 63(6): 942–956. (in Chinese)
- Riutta T, Slade E M, Bebbler D P *et al.*, 2012. Experimental evidence for the interacting effects of forest edge, moisture and soil macrofauna on leaf litter decomposition. *Soil Biology and Biochemistry*, 49(6): 124–131. doi: 10.1016/j.soilbio.2012.02.028
- Sardans J, Rivas-Ubach A, Penuelas J, 2012. The C : N : P stoichiometry of organisms and ecosystems in a changing world: a review and perspectives. *Perspectives in Plant Ecology Evolution and Systematics*, 14(1): 33–47. doi: 10.1016/j.ppees.2011.08.002
- Saunders D L, Kalff J, 2001. Nitrogen retention in wetlands, lakes and rivers. *Hydrobiologia*, 443(1): 205–212. doi: 10.1023/A:1017506914063
- Schimel J P, Gullledge J M, Clein-Curley J S *et al.*, 1999. Moisture effects on microbial activity and community structure in decomposing birch litter in the Alaskan taiga. *Soil Biology and Biochemistry*, 31(6): 831–838. doi: 10.1016/S0038-0717(98)00182-5
- Song Xiaolin, Lu Xianguo, Liu Zhengmao *et al.*, 2012. Runoff change of Naoli River in Northeast China in 1955–2009 and its influencing factors. *Chinese Geographical Science*, 22(2): 144–153. doi: 10.1007/s11769-012-0525-1
- Tarnocai C, 2006. The effect of climate change on carbon in Canadian peatlands. *Global and Planetary Change*, 53(4): 222–232. doi: 10.1016/j.gloplacha.2006.03.012
- Tian H, Chen G, Zhang C *et al.*, 2010. Pattern and variation of C : N : P ratios in China's soils: a synthesis of observational data. *Biogeochemistry*, 98(1): 139–151. doi: 10.1007/s10533-009-938-0
- Vitousek P M, Aber J D, Howarth R W *et al.*, 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications*, 7(3): 737–750. doi: 10.1890/1051-0761(1997)007[0737:HAOTGN]2.0.CO;2
- Vitousek P M, Porder S, Houlton B Z *et al.*, 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. *Ecological Applications*, 20(1): 5–15. doi: 10.1890/08-0127.1
- Wang S Q, Tian H Q, Liu J Y *et al.*, 2003. Pattern and change of

- soil organic carbon storage in China: 1960s–1980s. *Tellus Series B-Chemical and Physical Meteorology*, 55(2): 416–427. doi: 10.1034/j.1600-0889.2003.00039.x
- Yu Q, Elser J J, He N *et al.*, 2011. Stoichiometric homeostasis of vascular plants in the Inner Mongolia grassland. *Oecologia*, 166(1): 1–10. doi: 10.1007/s00442-010-1902-z
- Zhao Kuiyi, 1999. *Chinese Marsh*. Beijing: Science Press. (in Chinese)