



Effects of submergence frequency on soil C:N:P ecological stoichiometry in riparian zones of Hulunbuir steppe

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Abstract

Purpose Hulunbuir steppe has flat terrain and wide riparian zone of rivers and lakes on it. Owing to climate change, these riparian zones are often submerged or dried. This not only results in the instability of biodiversity in these regions but also affects the soil biogeochemical cycles. Soil C:N:P ecological stoichiometry plays a vital role in predicting and understanding the balance of multiple chemicals in ecological interactions. However, few studies have examined the soil C:N:P ecological stoichiometry in riparian zones of Hulunbuir steppe under different submergence states. Our objectives were to explore whether submergence frequencies impact soil C:N:P stoichiometry and identify the key factors.

Materials and methods Four study sites were selected along the Hui river in Hulunbuir steppe, and three plots of different submergence frequencies, high (HF-sub, 5 to 7 times per year), moderate (MF-sub, 2 to 3 times per year), and low (LF-sub, unflooded or flooded once per year), were selected for each study site. Soil organic carbon (SOC), total nitrogen (TN), total phosphorus (TP), their ecological stoichiometric ratios (soil C:N, N:P, and C:P), soil ammonia nitrogen ($\text{NH}_4^+\text{-N}$), nitrate nitrogen ($\text{NO}_3^-\text{-N}$), available phosphorus (AP), soil pH, electrical conductivity (EC), soil moisture content (SMC), soil bulk density (SBD), porosity, and hardness were measured and analyzed.

Results and discussion The results indicated that soil C:N:P ecological stoichiometry was notably affected by submergence frequency across the four study sites ($P < 0.05$). SOC, TN, TP, and their stoichiometric ratios changed regularly with the submergence frequency change, whereas their trends were inconsistent at different drainage basins. Soil C:N decreased with the decrease in submergence frequency but kept in a narrow scope, whereas the N:P and C:P were changed greatly under different submergence frequencies. Further analysis found that these significant variations in N:P and C:P were mainly due to the changes in soil TP which suggested there might be a P limitation in the riparian zones. The results of redundancy analysis (RDA) and path analysis indicated that soil AP and $\text{NO}_3^-\text{-N}$ were the key indirect factors affecting soil C:N:P ecological stoichiometry under different submergence frequencies, and SMC was an indirect factor.

Conclusions We demonstrated that the soil C:N:P ecological stoichiometry was significantly affected by the submergence frequency in the riparian zones of Hulunbuir steppe. Soil N:P and C:P were more susceptible to change than C:N under different submergence frequencies. If the contents of soil AP and $\text{NO}_3^-\text{-N}$ were appropriate, soil C:N:P ecological stoichiometry will be more beneficial to regulating the cycle and balance of soil nutrient elements in the riparian zones, which can promote the riparian zones to provide better ecological functions.

Keywords Hulunbuir steppe · $\text{NO}_3^-\text{-N}$ · Soil AP · Soil C:N:P ecological stoichiometry · Submergence frequency

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1 Introduction

Hulunbuir steppe, located in Inner Mongolia of Northeast China, is the best preserved steppe in the eastern Eurasian steppe (Weger and Staalduinen 2012; He et al. 2017). The riparian zones formed by rivers or lakes are the transition and connection zones of grassland and rivers or lakes on the Hulunbuir steppe, which have abundant biodiversity, water,

and forage resources (Zhu et al. 2018, 2019). In the pastoral regions, herders live and herd their livestock around open areas of grassland according to seasons and the changing availability of water and pasture (Fernández-Giménez 1999). Due to high plant diversity and productivity as well as abundant water resources, the areas around the riparian zones are usually a better pasture and camp for herders, especially at the dry season: the forage productivity and plant diversity of the Hulunbuir steppe are weak and poor, whereas the riparian zones are vibrant and lush (Caihong et al. 2013; He et al. 2017). On the other hand, these riparian zones also are the important habitats and water and food resources for migratory birds and wildlife. However, due to climate change and anthropogenic disturbance, such as reclamation and overgrazing, most Hulunbuir steppes have severely degenerated in recent decades (Sun et al. 2016; Na et al. 2019; Zhao et al. 2019). In these degraded processes, the riparian zones were the most fragile and sensitive ecosystems, which reflected in the shrinkage of the riparian area, degradation of ecological functions, soil salinization, etc. (Wang et al. 2017; Na et al. 2019; Zhao et al. 2019).

Unlike other riparian zones, the riparian zones on the Hulunbuir steppe are relatively wide and flat. In the high-water period, such as the snowmelt season and rainy season, almost all the areas of the riparian zones are submerged by the flood from rivers or lakes, and the width of the submerged areas is approximately 200 to 300 m. However, in the withered water period, flood recedes and the water areas of rivers or lakes decrease rapidly, and the riparian zones are drained (Tonkin et al. 2018; Joseph et al. 2019; Larson et al. 2019). In this cycling of flooding and draining, the riparian zones suffer the periodic cycle of submergence and drought, and the frequency of submergence or drought varies in the land perpendicular to the river channel (Deslippe et al. 2014; Holt et al. 2017). The areas near the river channel or margin of the riparian zones are almost flooded or drained all year around, whereas between these two regions, submergence and de-submergence alternately cycle due to the fluctuation of the water table (Wu and Liu 2015). The difference of submergence frequency in the direction perpendicular to the river channel will greatly affect vegetation community composition, plant diversity, forage productivity, soil physicochemical properties, soil nutrient cycling, and even soil C:N:P stoichiometry of the riparian zones (Wilson et al. 2011; Jiang et al. 2015; Stromberg et al. 2017). However, the research focusing on the effect of submergence frequency on soil C:N:P ecological stoichiometry is limited (Ren et al. 2018; Wang et al. 2018b), particularly the riparian zones on grassland.

Soil ecological stoichiometric ratio (C:N:P) plays the most important role in revealing the cycling and equilibrium mechanisms of soil carbon (C), nitrogen (N), phosphorus (P), and other nutrient elements (Sinsabaugh and Follstad Shah 2012). It relates to the important soil biological processes, such as the

coupling and transformation of C, N, and P (Amoros and Bornette 2002; Li et al. 2018), and soil litter decomposition, as well as the biochemical cycle of nutrients and organic matter breakdown or oxidation (Sinsabaugh and Follstad Shah 2012). In riparian zones, the C:N:P stoichiometric ratio of soil or plants can be used as an indicator to evaluate the health quality of riparian zones (Huang et al. 2019); however, previous research studies mostly focused on exploring the effects of the changes in submergence frequency on the riparian zones' plant succession (Bourgeois et al. 2016), community structure (Garssen et al. 2015; Stromberg et al. 2017), invasive plant species (Pattison et al. 2019), soil erosion, physicochemical properties (Shu et al. 2017), C and N cycle (Fellows et al. 2011; Harrison-Kirk et al. 2014; Gao et al. 2018), eutrophication (Ricker and Lockaby 2015), greenhouse gas emissions (Jacinthe et al. 2015), etc. The literature studying on soil C:N:P stoichiometric ratio of the riparian zones on the Hulunbuir steppe was limited (Frost et al. 2005; Lin et al. 2013), particularly the effect of different submergence frequencies on the riparian zones' soil C:N:P ecological stoichiometry.

The flooding-draining alternation of riparian zones not only affects plant diversity and growth on the ground but also affects soil physical and chemical properties and soil C:N:P ecological stoichiometry. Therefore, in the present study, we selected four riparian zones with different submergence frequencies along the upper, middle, and lower reaches of the Hui river on the Hulunbuir steppe to explore the effects of submergence frequency on soil C:N:P ecological stoichiometry and its key control factors. The objective of this study is to investigate the response of soil C:N:P stoichiometry to different submergence frequencies and to identify the main soil physicochemical factors affecting soil C:N:P ecological stoichiometric ratios in order to provide a basis for the management of riparian ecosystems on the Hulunbuir steppe.

2 Materials and methods

2.1 Study region description

The current research was conducted in Huihe National Nature Reserve, Hulunbuir steppe, northeastern China, with a latitude of 48° 10'–48° 57' N and longitude of 118° 48'–119° 45' E, which had a total area of 3468 km². This region is strongly affected by the temperate continental monsoon climate and has an annual average temperature of –2.4 to 2.2 °C. The frost-free period is 100 to 120 days, and the annual average precipitation (2008 to 2014 years) is 375 mm, 70% of which falls in June to September of each year. The nature reserve is one of the 151 critical areas for biodiversity protection that joined the China Biosphere Reserve Network (CBRN) in 2007. In this reserve, Hui river crosses the whole reserve.

Influenced by the landforms of Hulunbuir steppe, the riparian zones of Hui river are broad and flat, approximately 50 to 300 m in width. These broad riparian zones are abundant in water, food, and biodiversity and are an ideal habitat for migratory birds. Due to locating in the core zone of the reserve, the riparian zone of Hui river is less disturbed by anthropogenic activities except local herders, livestock, and wild animals, is relatively primitive, and has a high species richness. The vegetation community is mainly constituted by Gramineae, Asteraceae, and Cyperaceae, such as *Agrostis alba*, *Phragmites communis*, *Leymus chinensis*, and *Carex Linn*. Scattered shrubs are occasionally found in the riparian zones near the river channel, such as *Tamarix ramosissima*. The soils in the riparian zones of Hui river are classified as Fluvisols and Kastanozems (WRB 2015).

2.2 Experimental design and soil sampling

Due to the flat topography and continuous landscape of Hulunbuir steppe, the landforms and soil types of Hui river's riparian zones change slightly in response to longitudinal variability. However, due to the differences in the flooding frequency and hydraulic energy in the direction perpendicular to the river channel, the soil and vegetation types sharply change in response to transversal variability. Our field survey identified four sites with similar landforms and soil types in the direction perpendicular to the river channel, and they were covered by native species, including *Carex Linn*, *Phragmites australis*, and *Leymus chinensis*. Muqiao (MQ) (48° 27' 17.2" N, 119° 02' 28.8" E) located in the upstream of the Hui river was 667.2 m above sea level, with 65% vegetation coverage and 6.7 cm average community height, a nearly 3° slope, and 130 m average riparian width. Chagan mountain (CGM) (48° 36' 30.1" N, 118° 52' 56.5" E) located in the midstream and average elevation was 657.6 m, with 80% grass cover and 45.3 cm average height, a less than 3° slope, and 200 m average riparian width. Xiboqiao (XBQ) (48° 49' 29.1" N, 119° 13' 49.1" E) located in the mid-downstream was 641.5 m, with 70% coverage and 25.3 cm average community height, a flat slope, and 170 m average riparian width. Temohuzhu (TMHZ) (48° 55' 24.4" N, 119° 40' 20.0" E) located in the downstream and elevation was 637.4 m, with 50% grass cover and 10.3 cm average community height, a flat slope, and approximately 200 m riparian width (Fig. 1).

In each study site, three replicate transects that were oriented perpendicular to the river channel were established, spaced 3 m (Fig. 1), totally 12 transects in the four study sites. According to interviewing native residents and historical data, we developed a submergence frequency schedule to match natural conditions. Using this schedule, three 2 m × 2 m study plots were developed within each transect, totally 36 study plots. The plots close to the river stream were frequently submerged approximately 5 to 7 times per year with high

hydraulic energy (high-frequency submergence, henceforth HF-sub). They were about 10 m, 20 m, 15 m, and 20 m from the river flow at MQ, CGM, XBQ, and TMHZ sites, respectively (Fig. 1). The plots farther from the river were submerged approximately 2 to 3 times per year with low hydraulic energy (moderate-frequency submergence, MF-sub). They were about 60 m, 90 m, 80 m, and 90 m from the HF-sub plots at MQ, CGM, XBQ, and TMHZ, respectively. The plots near the riparian margin were far from MF-sub plots and were unflooded or flooded once per year (low-frequency submerged, LF-sub). They were approximately 50 m, 70 m, 65 m, and 80 m from the MF-sub plots at MQ, CGM, XBQ, and TMHZ, respectively (Fig. 1). Due to the differences in flooding frequency and hydraulic energy in the direction perpendicular to the river channel, in the HF-sub areas, the soil is frequently affected by flooding with high hydraulic energy; the soil type is Arenic Fluvisols (WRB 2015). In the MF-sub areas, the soil is occasionally flooded with low hydraulic energy; the soil type is Humic Fluvisols (WRB 2015). In the LF-sub areas, the soil is almost unaffected by flooding or is only submerged once per year; the soil type is similar to the grassland soil and is classified as Kastanozems (WRB 2015). About 15 days after the submergence event receded in the HF-sub areas, soil samples (0–30 cm) were collected during August 1 to August 7, 2018. Because the soil was heterogeneous, three soil samples were collected from each sampling plot using the soil auger, obtaining a total of 27 soil samples from each study site. Then each soil sample was immediately divided into two after removing the visible roots, residues, and stones. Half of each sample was stored at 4 °C to measure soil ammonia nitrogen (NH₄⁺-N), nitrate nitrogen (NO₃⁻-N), available phosphorus (AP), soil pH, and electrical conductivity (EC). Another half of each sample was shipped to the laboratory and then air-dried, crushed, sieved, and used to analyze soil organic carbon (SOC), total nitrogen (TN), and total phosphorus (TP). To determine soil moisture content (SMC), soil bulk density (SBD), and total porosity, undisturbed soil samples (0–10 cm, 10–20 cm, and 20–30 cm) were also collected from the same plots using a thin-walled steel cylinder of 5 cm height and 100 cm³ volume. Three repeats were collected in each soil layer, getting a total of 81 undisturbed soil cores from each study site. A total of 324 soil cores from all study sites were collected for determining soil physical properties.

2.3 Soil physicochemical analysis

SOC (g kg⁻¹) contents were examined using the potassium dichromate-sulfuric acid oxidation method (Lu 1999). TN (g kg⁻¹) was measured by the Kjeldahl method. TP (g kg⁻¹) was determined by the colorimetric method (Murphy and Riley 1962) using the sulfuric acid digestion procedure, whereas AP (mg kg⁻¹) was extracted using 0.5 M NaHCO₃

by colorimetric Assyrian at 880 nm. Soil $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ were extracted using 2 M KCl, then the mixture was

filtered, and $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ in the filtrate were analyzed colorimetrically using a flow injection analyzer (QuikChem

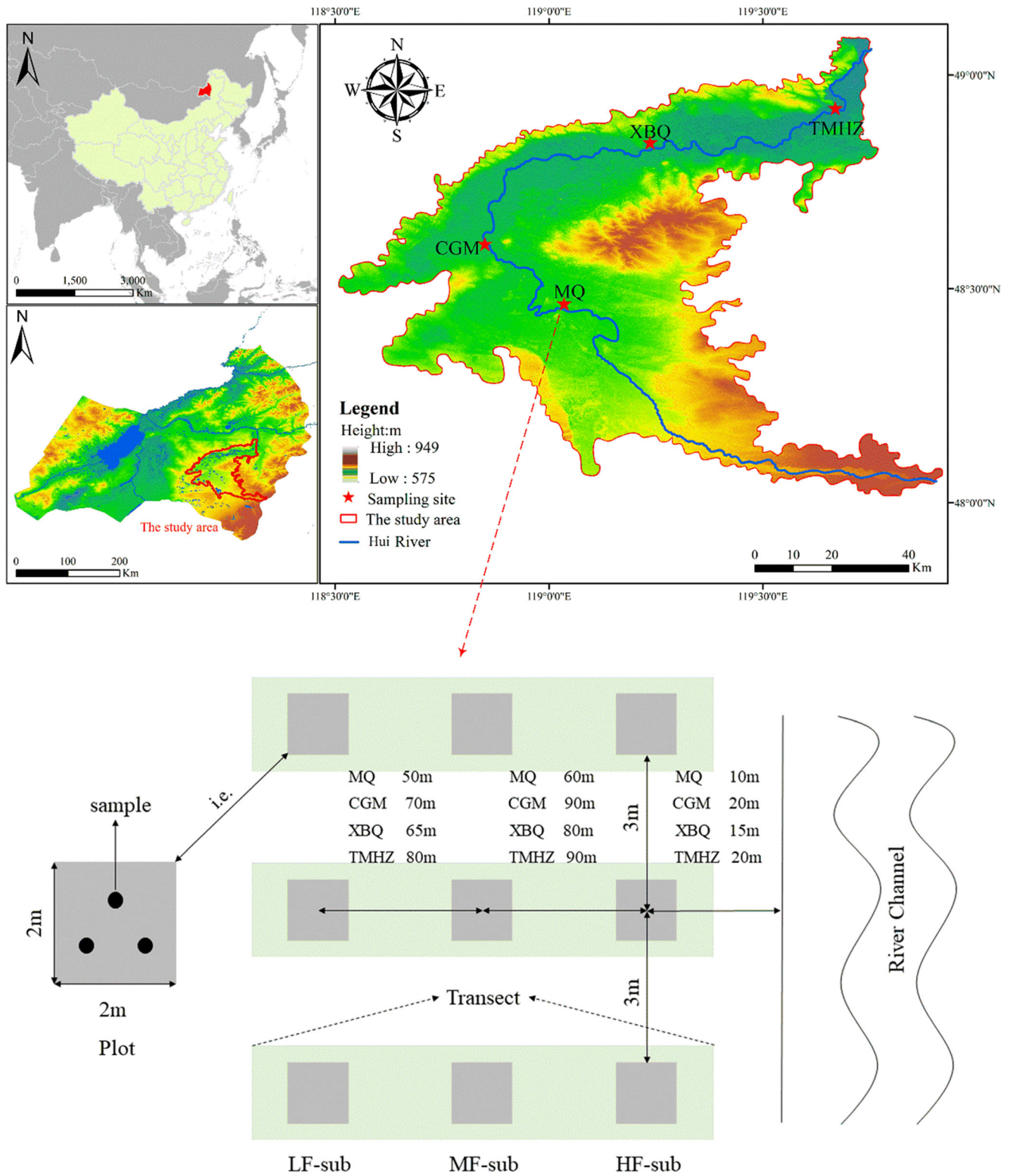


Fig. 1 Study site locations (MQ, CGM, XBQ, and TMHZ) and field sampling schematic diagram under different submergence frequencies, in Hulunbuir, Inner Mongolia, China. MQ, Muqiao; CGM, Chagan mountain; XBQ, Xiboqiao; TMHZ, Temohuzhu; HF-sub, high-

frequency submergence (5 to 7 times per year); MF-sub, moderate-frequency submergence (2 to 3 times per year); LF-sub, low-frequency submergence (unflooded or flooded once per year)

8000, Hach Company, Loveland, CO, USA). Soil pH values were measured electrometrically using an Orion Model 720A pH meter in water at a ratio of 1:2.5 (mass/volume). Soil EC ($\mu\text{S cm}^{-1}$) was determined using a conductivity meter in water at a ratio of 1:2.5 (mass/volume).

The undisturbed soil cores were used to evaluate SMC (%) and SBD (g cm^{-3}) at 105 °C for 24 h. Soil total porosity (%) was calculated using values of SBD and particle density which was assumed to be 2.65 g cm^{-3} . Soil hardness (kg cm^{-2}) (0–10 cm, 10–20 cm, and 20–30 cm) was measured using a manual Eijkelkamp penetrometer (Zadorozhnaya et al. 2018), four repeats at each soil layer.

2.4 Statistical analysis

One-way analysis of variance (ANOVA) was used to compare the differences in soil C:N:P ecological stoichiometry (including SOC, TN, TP, C:N, N:P, and C:P) and soil physicochemical properties ($\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, AP, soil pH, SMC, SBD, EC, soil total porosity, and soil hardness) for each submergence frequency (HF-sub, MF-sub, and LF-sub) within the study sites, and we then used Fisher's least significant difference (LSD) test to compare the average values. Because of the four study sites from different watersheds of the Hui river and with different altitudes, we used to two-way ANOVA to analyze the influences of the different submergence frequencies, study sites, and interactions of these factors on soil C:N:P ecological stoichiometry. To visualize the group separation of soil C:N:P ecological stoichiometry under different submergence frequencies at the four sites, the discriminant function analysis (DFA) was conducted. DFA is a statistical analysis used to predict a categorical dependent variable (called a grouping variable) by one or more continuous or binary independent variables (called predictor variables) (Rutherford 2003). The model is composed of a discriminant function based on linear combinations of independent variables, and those independent variables provide the best discrimination between groups. DFA is used to maximally separate the groups, to determine the most parsimonious way to separate groups or to discard variables which are little related to group distinctions. DFA is similar to regression analysis. A discriminant score can be calculated based on the weighted combination of the independent variables. Soil C:N:P ecological stoichiometry as independent variable to calculate discriminant functions and the squared Mahalanobis distances between group centroids were determined. In order to determine the relationship between soil C:N:P ecological stoichiometry and physicochemical properties, a redundancy analysis (RDA) was conducted. Through the RDA, we screened the significant physicochemical factors affecting soil C:N:P ecological stoichiometry. Then, to further clearly visualize the relationships between soil physicochemical properties and soil

C:N:P ecological stoichiometry, a confirmatory path analysis was conducted using these significant physicochemical factors and soil C:N:P ecological stoichiometry by R “lavaan” and “semPlot” packages. All statistical tests were at a 0.05 significance level except otherwise stated. The statistical tests were performed using OriginPro v. 2015 (OriginPro for Windows, ver. 2015; OriginLab, Northampton, MA, USA) and R. The RDA and path analysis were performed and graphed using Canoco software (Microcomputer Power, USA) and R, respectively, and the others were visualized using OriginPro v. 2015.

3 Results

3.1 Soil physicochemical properties

Soil physical properties (SMC, SBD, soil porosity, and hardness) greatly differed at different submergence frequencies among the four study sites (Fig. 2) ($P < 0.05$). At 0–30 cm soil depth, SMC and soil porosity of all study sites ranged from 70.7 to 18.5% and 73.8 to 42.4%, respectively, and with the increase in inundation frequency, these two parameters gradually increased but decreased with soil depth ($P < 0.05$). On the contrary, SBD and hardness ranged from 1.5 to 0.7 g cm^{-3} and 9.6 to 0.5 kg cm^{-2} , respectively, and increased with soil depth ($P < 0.05$) but decreased with submergence frequency ($P < 0.05$).

Soil $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, AP, pH, and EC were also significantly affected by the different submergence frequencies at the four study sites (Table 1) ($P < 0.05$). As the submergence frequencies increased, soil $\text{NH}_4^+\text{-N}$ notably decreased, whereas soil pH and EC increased ($P < 0.05$). In contrast, soil $\text{NO}_3^-\text{-N}$ increased first and then decreased with the increase in submergence frequencies at the four study sites ($P < 0.05$). Soil AP was obviously different ($P < 0.05$) under different submergence frequencies but irregular with the change in submergence frequencies.

3.2 Soil C:N:P ecological stoichiometry

The variations in SOC, TN, TP, soil C:N, N:P, and C:P were significantly different under different submergence frequencies among the four studied sites (Fig. 3) ($P < 0.05$). SOC and TN showed similar trends to different submergence frequencies at the four studied sites. For example, SOC and TN increased initially but then decreased from HF-sub to LF-sub at CGM, whereas decreased continuously from HF- to LF-sub at XBQ and TMHZ. TP also increased initially then decreased, but except at the TMHZ site.

Soil C:N changed in a narrow scope (5.5 to 12.1) but was significant ($P < 0.05$) (Fig. 3). It notably increased with the decrease in submergence frequency from HF- to LF-sub at

MQ, whereas decreased with the frequency change at CGM, XBQ, and TMHZ. Soil N:P and C:P greatly fluctuated under different submergence frequencies. For example, as the submergence frequency decreased, they obviously decreased initially but then increased at MQ and XBQ sites, whereas at CGM site, they continuously decreased ($P < 0.05$) even the variabilities were slighter than those of other sites,

Two-way ANOVA showed that the interactions between submergence frequency and study site were significant (Table 2) ($P < 0.01$). Overall, SOC, TN, and TP significantly increased initially and then decreased from HF- to LF-sub and also from upstream (MQ) to downstream (TMHZ) under the same submergence frequency. Soil C:N:P decreased as the submergence frequency decreased, whereas increased from upstream to downstream, even though C:P and N:P greatly fluctuated.

3.3 DFA of soil C:N:P ecological stoichiometry

DFA results of SOC, TN, TP, soil C:N, N:P, and C:P under different submergence frequencies were graphically described in two dimensions (Fig. 4). The DFA results showed that 79.6%, 90.0%, 97.2%, and 92.0% of the variance of the investigated dataset can be correctly classified by DFA at MQ, CGM, XBQ, and TMHZ, respectively. Interestingly, HF-sub and both MF-sub and LF-sub were almost completely separated by canonical variable 1 at the four studied sites, and the separation of MF-sub and LF-sub was illustrated by canonical variable 2 at CGM, XBQ, and TMHZ. The separation by canonical variable 2 was weaker than that by canonical variable 1. It was observed that the centroid of the MF-sub group was closer to that of HF-sub than to that of LF-sub at all study sites. The contribution of SOC, TN, TP, soil C:N, N:P, and C:P to the

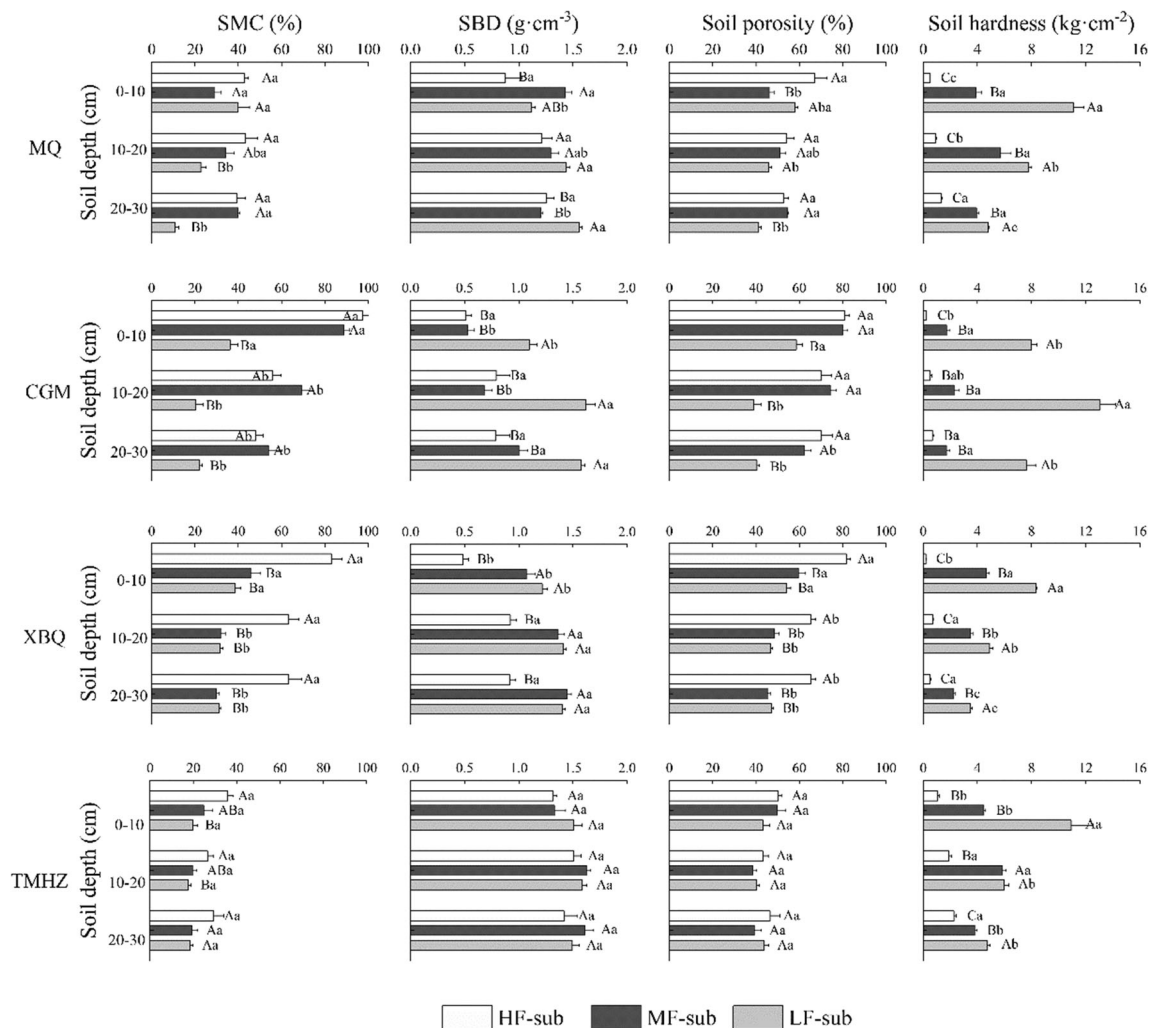


Fig. 2 Soil physical characteristics under different submergence frequencies, high-frequency submergence (HF-sub, 5 to 7 times per year), moderate-frequency submergence (MF-sub, 2 to 3 times per year), and low-frequency submergence (LF-sub, unflooded or flooded once per year), at four study sites (MQ, CGM, XBQ, and TMHZ). Capital letters (A > B > C) above the mean \pm SE represent differences

between different submergence frequencies at each study sites under the same soil layer (LSD test, $P < 0.05$), and lowercase letters (a > b > c) indicate discrepancies between different soil layers at each study sites under the same submergence frequencies (LSD test, $P < 0.05$). SMC, soil moisture content; SBD, soil bulk density

Table 1 Soil chemical properties under different submergence frequencies (HF-sub, MF-sub, and LF-sub) at the four study sites (MQ, CGM, XBQ, and TMHZ)

| Site | Condition | NH ₄ ⁺ -N (mg kg ⁻¹) | | | NO ₃ ⁻ -N (mg kg ⁻¹) | | | AP (mg kg ⁻¹) | | | pH | | EC (μs cm ⁻¹) | | | |
|------|-----------|--|----|-------|--|---|-------|---------------------------|---|-------|-----|---|---------------------------|-------|----|--------|
| MQ | HF-sub | 21.6 | a | (0.5) | 13.1 | b | (0.2) | 6.8 | c | (0.3) | 7.5 | b | (0.0) | 122.1 | c | (3.4) |
| | MF-sub | 17.1 | b | (0.5) | 27.0 | a | (1.1) | 39.8 | a | (0.6) | 7.6 | b | (0.0) | 167.4 | b | (4.4) |
| | LF-sub | 6.3 | c | (0.5) | 11.3 | b | (0.1) | 14.2 | b | (0.1) | 8.5 | a | (0.1) | 238.9 | a | (8.6) |
| CGM | HF-sub | 9.5 | a | (0.7) | 28.7 | b | (0.4) | 28.7 | b | (1.1) | 7.6 | c | (0.1) | 119.2 | a | (11.8) |
| | MF-sub | 9.5 | a | (1.2) | 53.1 | a | (1.0) | 31.2 | b | (1.1) | 7.9 | b | (0.0) | 149.8 | a | (8.3) |
| | LF-sub | 6.8 | a | (0.7) | 17.5 | c | (0.9) | 37.8 | a | (0.7) | 8.5 | a | (0.0) | 137.7 | a | (7.3) |
| XBQ | HF-sub | 11.1 | a | (1.0) | 21.4 | b | (3.1) | 13.6 | a | (0.0) | 8.5 | a | (0.0) | 121.1 | b | (7.5) |
| | MF-sub | 7.9 | b | (0.3) | 32.8 | a | (0.8) | 10.1 | b | (0.4) | 8.5 | a | (0.0) | 201.0 | ab | (10.2) |
| | LF-sub | 3.8 | c | (0.2) | 13.2 | c | (0.4) | 8.2 | c | (0.3) | 8.6 | a | (0.2) | 213.8 | a | (42.4) |
| TMHZ | HF-sub | 12.7 | a | (0.3) | 19.8 | b | (0.6) | 6.2 | b | (0.1) | 8.3 | b | (0.0) | 211.8 | b | (3.5) |
| | MF-sub | 11.1 | ab | (1.2) | 23.1 | a | (0.0) | 5.8 | b | (0.1) | 8.4 | b | (0.0) | 213.7 | b | (2.3) |
| | LF-sub | 8.7 | b | (1.1) | 14.5 | c | (0.5) | 7.6 | a | (0.1) | 8.8 | a | (0.1) | 309.8 | a | (7.4) |

Data are average and standard error (in parenthesis). Different lowercase letters behind the average represent significant difference (LSD test, $P < 0.05$). MQ, Muqiao; CGM, Chagan mountain; XBQ, Xiboqiao; TMHZ, Temohuzhu; NH₄⁺-N, soil ammonium nitrogen; NO₃⁻-N, soil nitrate nitrogen; AP, soil available phosphorus; EC, soil electrical conductivity. HF-sub means high-frequency submergence (submerged 5 to 7 times per year); MF-sub means moderate-frequency submergence (submerged 2 to 3 times); and LF-sub means low-frequency submergence (unflooded or flooded once per year)

calculated functions was different. Appendix 1 ([Electronic Supplementary Material](#)) shows that function 1 was dominated by soil C:P and function 2 was mainly affected by N:P and C:N at MQ. Function 1 of CGM was dominated by soil C:N, N:P, and C:P, whereas function 2 was dominated by SOC, TN, and TP. Soil C:N dominated function 1, whereas N:P and C:P dominated function 2 at XBQ and TMHZ. Overall, the separation of the soil C:N:P ecological stoichiometry in function 1 was mainly dominated by soil C:P and C:N, particularly C:P under the different submergence frequencies at the four study sites, whereas function 2 was mainly affected by soil N:P.

3.4 Effects of soil physicochemical properties on soil C:N:P ecological stoichiometry

RDA was used to explain the relationship among soil physicochemical properties and soil C:N:P ecological stoichiometry under different submergence frequencies (HF-sub, Fig. 5A; MF-sub, Fig. 5B; LF-sub, Fig. 5C; a summary of the three submergence frequencies, Fig. 5D) at the four study sites. To clearly visualize the RDA results, only the soil physicochemical properties with $P < 0.05$ were showed in Fig. 5A–D. The RDA eigenvalues indicated that most of the variances under HF-sub (Fig. 5A), MF-sub (Fig. 5B), and LF-sub (Fig. 5C) were explained by axis 1 (83.2%, 85.7%, and 93.3% for Fig. 5A–C, respectively), whereas the Fig. 5D was mainly explained by axis 2 (75.5%). The longer arrows mean the stronger correlation (Kennedy et al. 2005). The RDA results showed that SMC, NH₄⁺-N, NO₃⁻-N, AP, and pH had higher effects on soil C:N:P ecological stoichiometry, especially AP, under different submergence frequencies among the four studies sites (Fig. 5).

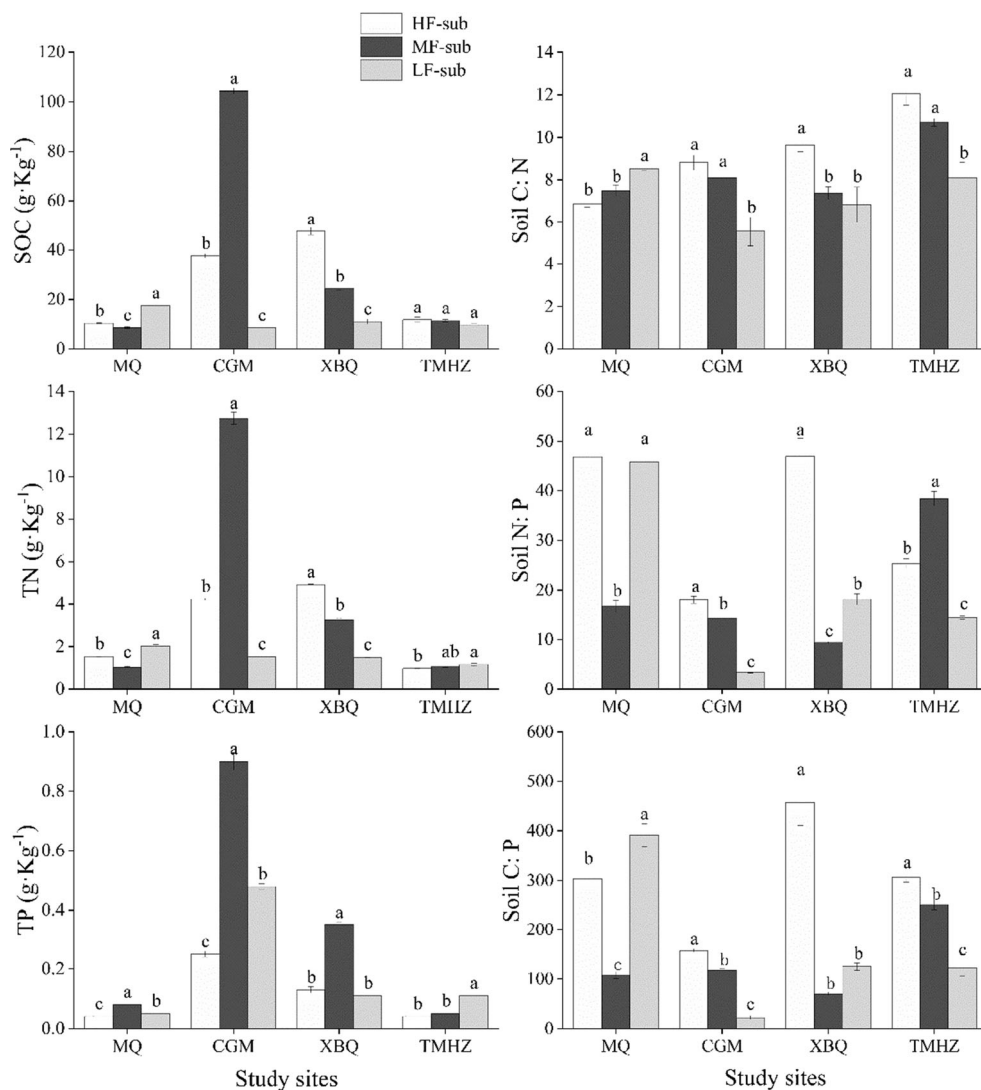
To further clarify the relationship between soil physicochemical properties and soil C:N:P ecological stoichiometry under different submergence frequencies, the path analysis was conducted, and only the physicochemical factors with $P < 0.05$ in the RDA were used in the path analysis (Fig. 6). Because the differences of submergence frequencies directly cause the differences in soil moisture content (SMC) in the direction perpendicular to the river channel, so we defined SMC as an endogenous variable, defined SOC, TN, TP, C:N, N:P, and C:P as the exogenous variables, and defined soil hardness, NH₄⁺-N, NO₃⁻-N, AP, and pH as the mediator variables in the path analysis. Figure 6 (CFI = 0.928, TLI = 0.750, and P value < 0.0001) shows that SMC significantly and positively affected soil AP and NO₃⁻-N but negatively affected soil NH₄⁺-N, hardness, and pH ($P < 0.01$). Both soil AP and NO₃⁻-N obviously positively ($P < 0.01$) influenced SOC, TN, and TP, especially NO₃⁻-N. Soil AP significantly negatively affected soil C:N, N:P, and C:P, especially N:P and C:P ($P < 0.01$). In addition, SOC, TN, TP, and their stoichiometric ratios were also indirectly affected by SMC, soil hardness, and pH, and the latter two factors also notably affected soil AP and NO₃⁻-N ($P < 0.01$).

4 Discussion

4.1 Variation in soil C:N:P ecological stoichiometry

Previous research has found that water level fluctuations are major events which affect riparian ecosystem of river and lakes (Hirabayashi et al. 2013; Shu et al. 2017; Luo et al. 2018). Soil physicochemical properties, nutrients, and

Fig. 3 Soil carbon, nitrogen, and phosphorus characteristics under different submergence frequencies (HF-sub, MF-sub, and LF-sub) at four study sites (MQ, CGM, XBQ, and TMHZ). Lowercase letters ($a > b > c$) above the mean \pm SE indicate differences at $P < 0.05$ using Fisher’s least significant difference (LSD) test between different submergence frequencies at each study sites. SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus



structure are significantly related with the frequencies of the water level fluctuations (Shu et al. 2017). In this study, we found that SOC, TN, and TP changed regularly as the submergence frequency changed, whereas their trends were inconsistent at different drainage basins. At the midstream riparian zones (CGM), SOC, TN, and TP increased initially but

then decreased from HF-sub to LF-sub. This might be resulted by the changes in soil organic matter content, litters, concentrations of nutrients, texture, porosity, aggregate stability, and redox potential due to the long-standing and frequent submergence and de-submergence events (Baastrup-Spohr et al. 2016; Shu et al. 2017; Yan et al. 2019). At the HF-sub areas

Table 2 Two-way ANOVA analysis for soil C:N:P ecological stoichiometry

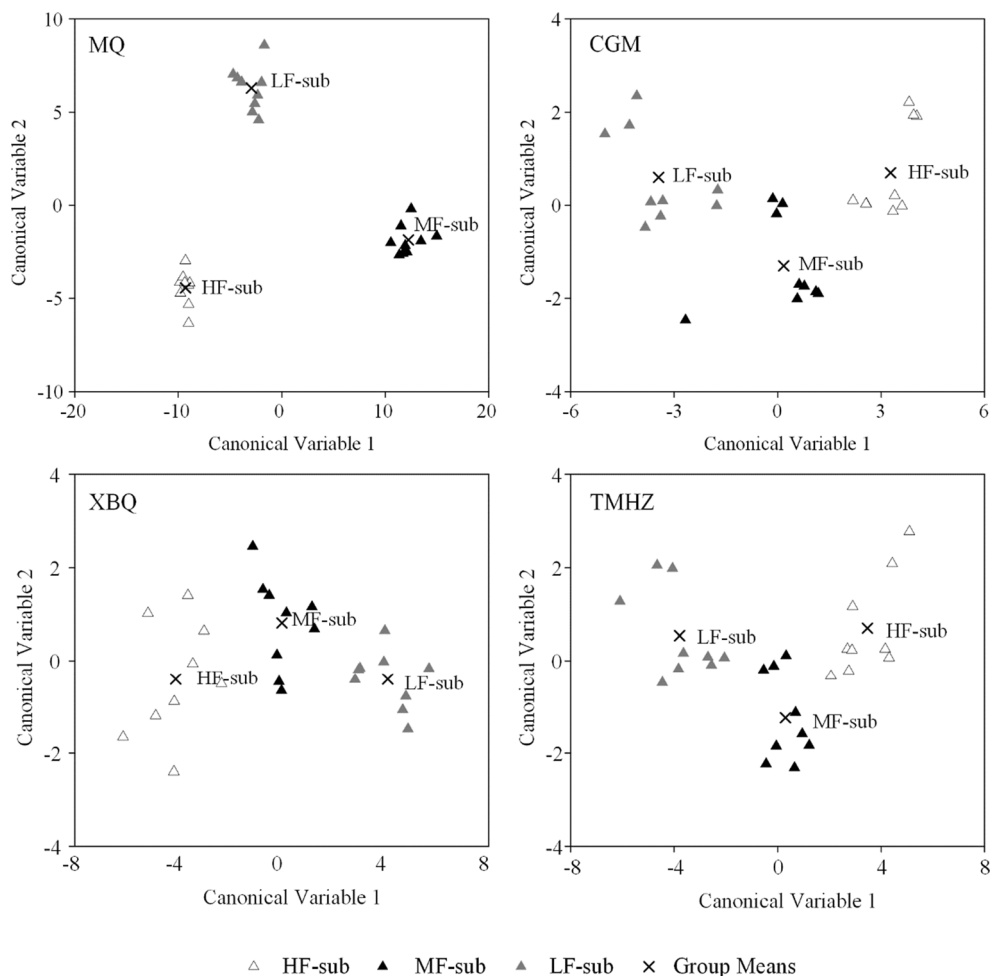
| Factor | SOC | TN | TP | C:N | C:P | N:P |
|-----------------------|------------|------------|------------|------------|------------|------------|
| Submergence (Sub) | 1035.0** | 1146.6** | 539.3** | 19.9** | 72.3** | 36.1** |
| Sub (sig) | b, a, c | b, a, c | c, a, b | a, a, b | a, a, b | a, a, b |
| Site (S) | 1378.1** | 1878.4** | 1587.9** | 26.8** | 173.5** | 88.7** |
| S (sig) | c, a, b, c | c, a, b, d | c, a, b, c | b, b, b, a | b, d, c, a | a, c, b, a |
| Interaction (Sub × S) | 985.7** | 1133.1** | 243.5** | 8.6** | 198.7** | 111.2** |

The categorical factors are submergence frequency (HF-sub: submerged 5 to 7 times per year, MF-sub: submerged 2 to 3 times per year, LF-sub: unflooded or flooded once per year) and study sites (MQ, CGM, XBQ, and TMHZ) and their interactions. Data are F values and level of significance (** $P < 0.01$). Lowercase letters indicate difference ($P < 0.05$). Sub (sig) represents discrepancies among different submergence frequencies. S (sig) represents discrepancies among study sites. SOC, soil organic carbon; TN, soil total nitrogen; TP, total phosphorus

of the upper or middle stream of the river, the hyporheic exchange and hydrologic pulsing are common and have high hydraulic energy (Shrestha et al. 2014), which will decrease soil porosity, oxygen content, redox ability (Lee et al. 2009) and then decrease soil physicochemical activity. These above changes can further weaken the transformation and decomposition of soil organic matter and litters and decrease the content of SOC (Lee et al. 2009), also affecting soil N cycling, such as decreasing N mineralization and increasing the denitrification due to the low porosity and oxygen (Nishio et al. 1993; Fellows et al. 2011), which will promote the soil N loss and decrease. On the other hand, the frequent hydrologic pulsing and high hydraulic energy can promote the movement of soil organic matter and plant residues from HF-sub to MF-sub areas (Viparelli et al. 2015), resulting in decreased contents of SOC, TN, and TP at HF-sub areas, whereas increased contents at MF-sub areas (Haywood et al. 2018). Meanwhile, the years of frequent and high-energy flooding pulsing will also gradually change soil types (Shu et al. 2017). For example, the soil type of MF-sub was gradually changed to Humic Fluvisols having thick litters and humus deposits. This type of soil has high porosity, biophysical activity, and nutrients such as high

SOC, TN, and TP (Kercheva et al. 2017). However, at the mid-downstream (XBQ sampling site) and downstream (TMHZ sampling site) of the river, the velocity of the river is slow. And the riparian zones of these drainage basins are flatter and broader than the upstream. Therefore, although the submergence and de-submergence are still frequent at HF-sub areas, the flooding energy and substance exchanges are weaker than the upstream, resulting in the deposits, litters, and nutrients remaining at the HF-sub areas rather than being transported to MF-sub areas (Li et al. 2017). This might be the reason why the contents of SOC, TN, and TP of HF-sub areas were higher than MF-sub and LF-sub areas at the mid-downstream and downstream of the river. In addition, at the MF-sub areas, the occasional submergence can promote the decomposition and mineralization of soil organic matter and residues (Nguyen and Lehmann 2009, Harrison-Kirk et al. 2014), which resulted in the gradually decrease of contents of SOC, TN, and TP. However, at the LF-sub areas of the whole river basin, the soil was almost unflooded or only once per year, and the soil type was similar to the grassland soil having lower nutrients, better porosity, physicochemical activity, and organic matter mineralization cycling than the other

Fig. 4 Calculated discriminant function analysis (DFA) under different submergence frequencies (HF-sub, MF-sub, and LF-sub) among the four study sites (MQ, CGM, XBQ, and TMHZ)

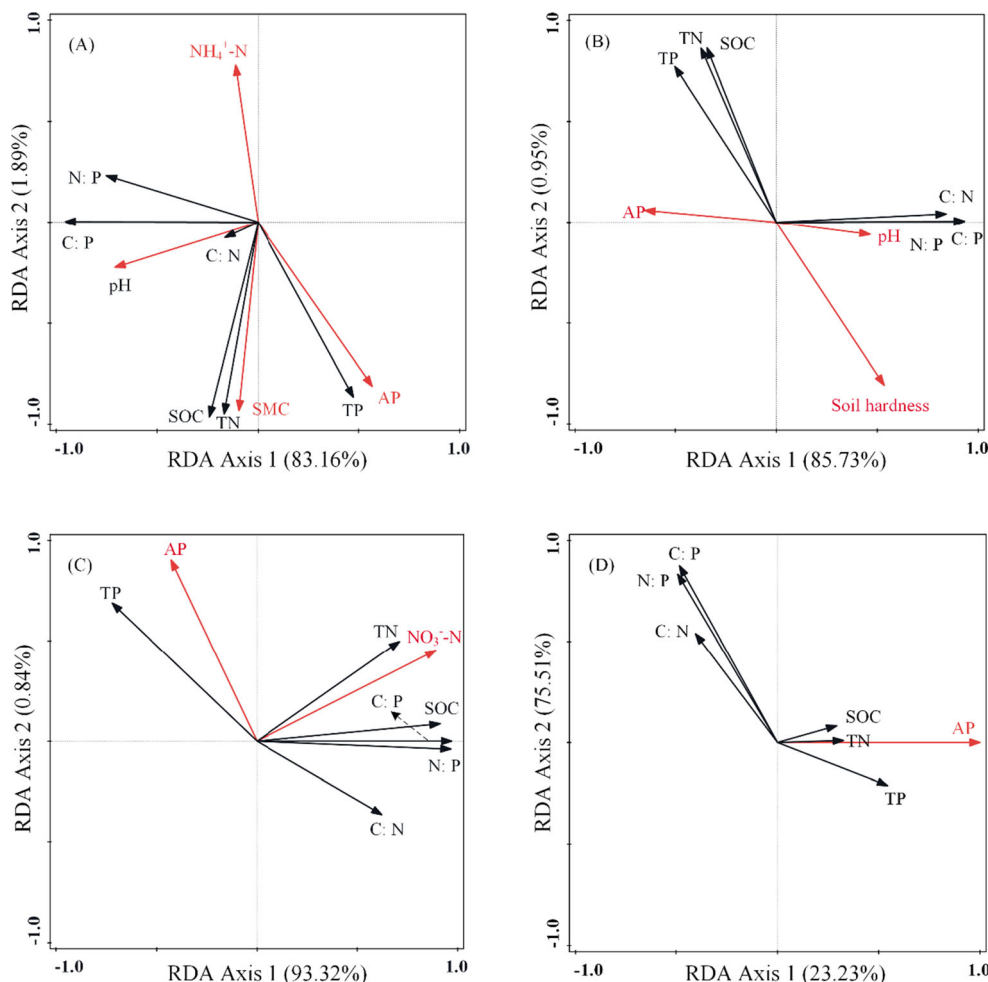


two submergence conditions. This might explain why the content of SOC, TN, and TP significantly decreased with the decrease in submergence frequencies, particularly at XBQ and TMHZ sites.

C, N, and P biologically coupled through their effects on the biogeochemical cycle that controls the process of respiration, photosynthesis, and decomposition in the terrestrial ecosystems (Finzi et al. 2011; Peñuelas et al. 2013). Compared with the absolute value of SOC, TN, and TP, the variation in soil C:N:P ecological stoichiometry is more meaningful in ecology (Agren 2004). It plays a vital role in predicting and understanding the balance of multiple chemicals in ecological interactions (Cleveland and Liptzin 2007; Elser et al. 2008). In the present study, our results showed that soil C:N kept in a narrow scope (5.5 to 12.1) although the submergence frequency changed greatly. Overall, soil C:N significantly decreased with the decrease in submergence frequency from HF- to LF-sub areas. The lowest soil C:N found in LF-sub areas can be explained by the low contents of SOC (Wang et al. 2018b). In addition, the low soil C:N (< 12) also implied the that there might be a relatively constrained C:N in the topsoil of our study areas and a feedback between soil and their biotas

(Zhang and Elser 2017; Delgado-Baquerizo et al. 2018), especially at the LF-sub areas. The relatively lower disturbance frequency, which resulted in the stable soil physicochemical and biological properties and biogeochemical cycle (Kogel-Knabner et al. 2010; Shu et al. 2017), might be the key factor leading to the relatively stable soil C:N. However, the N:P and C:P varied significantly with the submergence frequency change at the four study sites, particularly at MQ and XBQ sites. This can be explained by the opposite response trends of soil TN and TP to the changes in submergence frequency. For example, soil TN decreased initially and then increased from HF- to LF-sub at MQ, whereas soil TP increased initially and then decreased (Fig. 3). On the other hand, the high N:P and C:P values, as well as their great variability, might mainly be due to the low P contents and great P variability, which might imply that there was a P limitation (Wei et al. 2017). Soil P mainly comes from soil parent materials and is easy to be the precipitates, which results in a decrease in effectiveness of P element (Lambers et al. 2015). The long-term anaerobic or frequent flooding events caused an increase in the dissolution and diffusion for soil P, which further led to a decrease in P and high C:P and N:P (Wei et al. 2017). Furthermore, the

Fig. 5 Redundancy analysis (RDA) for the relationship between soil physicochemical properties and C:N:P ecological stoichiometry (including SOC, TN, TP, C:N, N:P, and C:P) under different submergence frequencies (HF-sub, MF-sub, and LF-sub) among the four study sites (MQ, CGM, XBQ, and TMHZ). In (A–D) the black line arrows indicate soil C:N:P ecological stoichiometry and the red line arrows indicate soil physicochemical properties with $P < 0.05$ were showed in (A–D). The RDA for the relationship between soil physicochemical properties and soil C:N:P ecological stoichiometry was (A) under HF-sub of the four study sites, (B) under MF-sub, (C) under LF-sub, and (D) under the three submergence frequencies. SOC, soil organic C; TN, total N; TP, total P; C:N = SOC:TN; N:P = TN:TP; C:P = SOC:TP; SMC, soil moisture content; $\text{NH}_4^+\text{-N}$, ammoniacal N; $\text{NO}_3^-\text{-N}$, nitrate N; AP available P; pH, soil pH



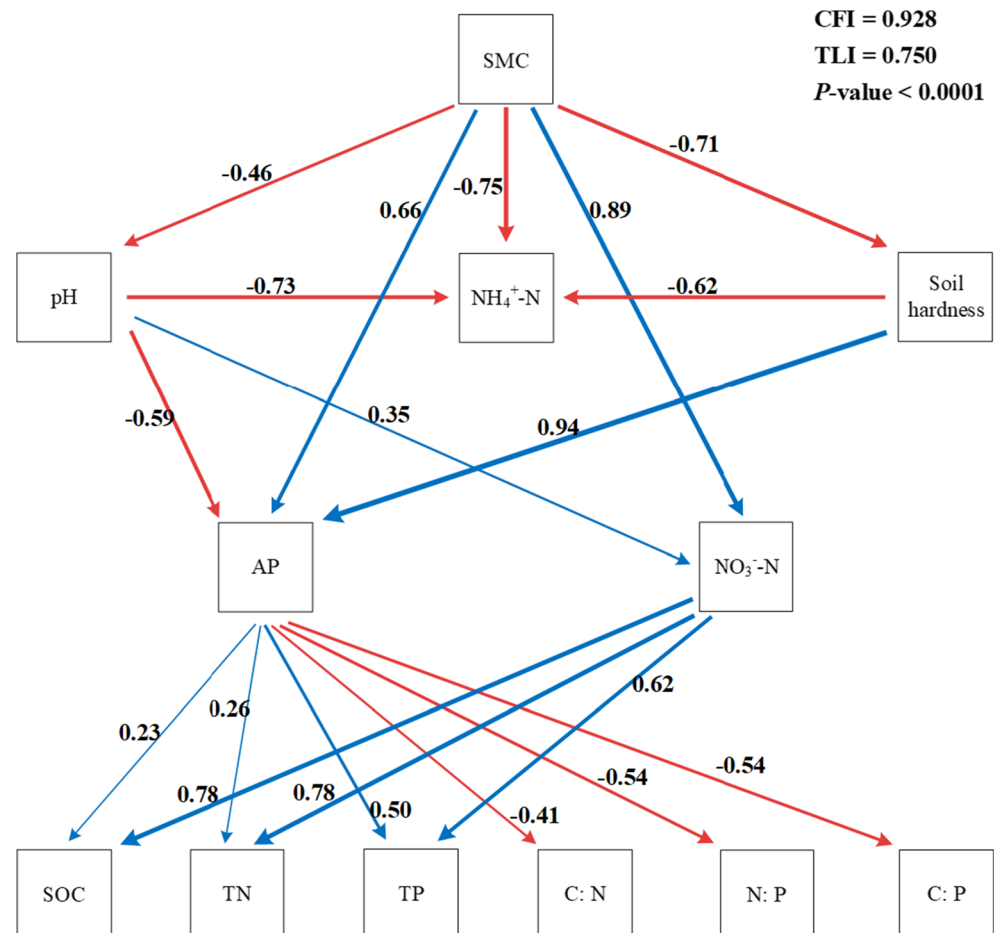
effectiveness of soil P was affected by soil pH and SMC. Drought and high soil pH can slow down the transport of phosphate ion, especially inorganic P, and promote the absorption by cations, particularly divalent cations, such as the Ca^{2+} , which further resulted in the utilization and cycling of decreased P (Jiao et al. 2016; Brodlin et al. 2019). These might be the reasons why the N:P and C:P were varied significantly. Through analyzing the datasets, we found that the average values of soil N:P (24.8 > 16) and C:P (202.7) values in the studied regions were higher than the average values of Chinese soils, i.e., 5.2 and 61, respectively (Tian et al. 2010), and also higher than the mean values found in wetland soils of Sanjiang Plain (12.8 and 162) (Zhang et al. 2012) and Dongting Lake (5.39 and 65.3) (Hu et al. 2017). These suggested that the cycling of soil nutrients was mainly limited by P in the riparian zones of Hui river on the Hulunbuir steppe.

4.2 The key soil physicochemical factors affecting soil C:N:P ecological stoichiometry

In riparian zones, the submergence frequency steadily decreases as the distance and altitude increased in the direction perpendicular to the river channel. When the soil is submerged, the

channel fluvial process from longitudinal and lateral flows created a heterogeneity in the soil physicochemical properties and soil nutrients (Wang et al. 2018a). The heterogeneity of soil physicochemical properties will affect the cycling of soil C, N, P, and their ecological stoichiometric ratios (Li et al. 2018). Consistent with previous research studies (Wang et al. 2015, 2018c), in this study, the results of RDA showed that soil NH_4^+ -N, NO_3^- -N, AP, pH, and hardness, particularly soil AP, were the main physicochemical factors affecting soil C:N:P ecological stoichiometry under different submergence frequencies. The results of path analysis showed that the difference in SMC in the direction perpendicular to the river channel, due to the change in submergence frequency, directly affected the changes in soil AP, NO_3^- -N, NH_4^+ -N, and hardness, which indirectly resulted in the change in soil C:N:P ecological stoichiometry. Also, the changes in soil AP and NO_3^- -N, especially AP, directly influenced soil C:N:P ecological stoichiometry. These results might imply that, in the direction perpendicular to the river channel, the differences in SMC caused by the changes in submergence frequency were the indirect factors causing the differences in soil C:N:P ecological stoichiometry, whereas the changes in AP and NO_3^- -N, especially AP, caused by the changes in SMC were the key direct factors affecting soil

Fig. 6 Path analysis for soil physicochemical properties and soil C:N:P ecological stoichiometry among the four study sites (MQ, CGM, XBQ, and TMHZ). Blue and red arrows indicate positive and negative relationships, respectively; numbers on the arrows indicate the standardized path coefficients, with arrow thickness proportional to the coefficient strength; and only the arrows with significant standardized path coefficients ($P < 0.01$) were showed. CFI, comparative fit index; TLI, Tucker-Lewis index. These two indexes were used to estimate the model of path analysis, and they are more near 1 mean better model



C:N:P ecological stoichiometry under different inundation frequencies in the riparian zones of Hui river on the Hulunbuir steppe. SMC is greatly related with soil physicochemical and biological activity (Shu et al. 2017). Both high and low SMC were not beneficial to soil biophysical activity and soil nutrient cycling, such as organic matter mineralization (Kercheva et al. 2017). These might explain why SMC directly affected soil AP, NO_3^- -N, and NH_4^+ -N and why soil AP and NO_3^- -N increased initially but then decreased. Moreover, the changes in soil physicochemical properties caused by SMC indirectly influenced soil C:N:P ecological stoichiometry (Wang et al. 2015). In this study, the great variabilities in soil N:P and C:P might mainly be caused by the P limitation. Relative to other macronutrients, soil P element is considerably less and is main source from phosphate rocks which is nonrenewable (Singh et al. 2015; Ahmed et al. 2018). Generally, 35–70% soil TP is inorganic P which is variable and easy to be bonded to metal oxides in acidic and highly weathered soils, such as submerged soil (Pritchett and Comerford 1982; Pierzynski et al. 2005). Soil AP is one of the main components of soil inorganic P (Sharpley 1985). Therefore, the changes in soil AP will have great effect on soil TP, N:P, C:P, and even C:N although the relationship between soil AP and TP is nonlinear (Delgado and Torrent 1997). These might explain why soil AP directly influenced soil C:N:P ecological stoichiometry. In addition, we found that soil hardness is also an important indirect factor affecting soil C:N:P through influencing the contents of soil AP. This might be due to the fact that soil hardness was closely related to soil texture, porosity, and nutrients transport which would indirectly influence the mineralization, adsorption, and ion diffusion of phosphates in soil (Kristoffersen and Riley 2005).

5 Conclusions

In the present study, we wanted to evaluate the response of soil C:N:P ecological stoichiometry to different submergence frequencies in the riparian zones of the Hui river on the Hulunbuir steppe and its main control factors.

Our data have demonstrated that the submergence frequency significantly affected soil physicochemical properties and soil C:N:P ecological stoichiometry. SOC, TN, TP, and their ecological stoichiometric ratios changed regularly with the submergence frequency change, whereas their trends were inconsistent at different drainage basins. Soil C:N was relatively stable, whereas the N:P and C:P were changed greatly under different submergence frequencies. The significant variations in N:P and C:P were mainly due to the changes in soil TP, which suggested there might be a P limitation in the riparian zones.

Soil AP, NH_4^+ -N, NO_3^- -N, pH, and hardness were the main physicochemical factors affecting soil C:N:P ecological stoichiometry under different submergence frequencies in the

riparian zones, where AP and NO_3^- -N were the key direct factors, and SMC was the indirect factor. Accordingly, we propose that if the contents of soil AP and NO_3^- -N were appropriate, soil C:N:P ecological stoichiometry will be more beneficial to regulating the cycle and balance of soil nutrient elements in the riparian zones, which can promote the riparian zones to provide better ecological functions.

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