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RESEARCH ARTICLE

Stoichiometric characteristics and homeostasis of leaf nitrogen and phosphorus responding to different water surface elevations in hydro-fluctuation zone of the Three Gorges Reservoir

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Abstract

As a type of wetland ecosystem with off-season 30 m water level fluctuation, the huge changes in the ecological environment, plant species, and vegetation dynamics in the hydro-fluctuation zone of the Three Gorges Reservoir (TGR) area have attracted a wide range of attention. In this present study, six typical locations in the water level fluctuating zone were used as the research objects, and the effects of different water surface elevations on the stoichiometric characteristics and homeostasis of leaf nitrogen and phosphorus were studied through a sample survey method. Results revealed that leaf nitrogen content was linearly correlated with leaf phosphorus content along water surface elevation. And water surface elevation significantly affected the nitrogen and phosphorus content of dominant plants. Four dominant species [*Cynodon dactylon* (Linn.) Pers, *Xanthium sibiricum* Partin ex Wider, *Abutilon theophrasti* Medik, and *Bidens pilosa* Linn] exhibited specific differences in the phosphorus steady state index (H_p) and nitrogen steady state index (H_N). Although belonging to different categories, both H_P and H_N of four dominant species were in the same order: *X. sibiricum* > *A. theophrasti* > *C. dactylon* > *B. Pilosa*. The interspecific differences in H_N and H_P indicated that there were differences in the characteristics of nutrient utilization of dominant species and their adaption to water surface elevation. Furthermore, as the elevation increases, the community coverage increased and the community stability index also increased. This might indicate that in the fluctuating zone habitat, the plant's nitrogen and phosphorus utilization strategy affects the distribution and composition of plant community along water surface elevation, and ultimately affects the stoichiometric homeostasis on the community levels.

Keywords Nitrogen and phosphorus stoichiometry · Stoichiometric homeostasis · Hydro-fluctuation zone · Three Gorges Reservoir Area

Introduction

As a powerful tool in ecology and biology, ecostoichiometry has been deeply applied to the assessment and interpretation of different ecosystems and ecological processes, such as individuals, populations, communities, and ecosystems (Sterner and Elser 2002; Han et al. 2005). A lot of studies have focused on the balance of chemical elements (Elser et al. 2009; Karimi and Folt 2006; Yu et al. 2011). Among them, the N/P ratio of plants can be widely used to judge nitrogen and phosphorus nutrient limitation to study the adaptability and stability of organisms to ecosystem changes (Güsewell 2004; He et al. 2008; Elser et al. 2009; Hu et al. 2014; Yu 2010, 2015; Tian et al. 2018).

Stoichiometric homeostasis, as a vital concept in ecological stoichiometry (Sterner and Elser 2002), depends on resource constraints, growth rates and growth constraints (Sistla et al. 2015). The stoichiometric homeostasis can reflect the potential physiological and biochemical distribution of biological reactions in the ecological system, and also reflects the ability of plants to sustain their own stability in different ecological environments (Elser et al. 2010; Yu et al. 2010). For example, species with a high steady-state index (H) are highly competitive and stable in terms

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of nutrition, while species with a low steady-state index (H), although growing faster and able to make full use of nutrients for growth in the case of adequate nutrition, are less stable and have a weak adaptability to the surrounding environment (Frost et al. 2005). Leaf steady-state index H is the most important stoichiometric characteristic to predict the success of plant species' competition and the diversity of resource supply (Yu et al. 2010; Sardans et al. 2012).

To date, a few studies have reported stoichiometric homoeostasis index (H) in terrestrial vascular plants (Güsewell 2004; Yu et al. 2010) and freshwater vascular plants (Li et al. 2013; Su et al. 2019). However, there are few studies on the ecological stoichiometric balance of plant species, the vegetation, and ecosystem in the hydro-fluctuation zone.

The Three Gorges Dam is mainly used to store water in summer with a water level of about 145 m, and in winter with a water level of about 175 m. In the continuous storage and release of water in the Three Gorges Reservoir (TGR) area, the water has formed a large water level difference and formed a significant hydro-fluctuation zone (Ye et al. 2011). This artificial water storage mechanism has led to significant changes in the ecological environment of the TGR area (Zhang et al. 2011). Under the fluctuation and disturbance of water level, these unstable factors led to further serious degradation of riparian ecosystem, leading to significant changes in plant community composition and structure (Wang et al. 2018). Under the influence of the fluctuation of water level, plants gradually degenerate after the flood disaster, but the vegetation exposed to the air grows and flourishes (Jian et al. 2018). Therefore, the life activities of the ecosystem in this region are very active, with biological diversity, frequent human activities and vulnerability of the ecological environment (Yin et al. 2019). Kong et al. (2020) reported the spatial variability of nutrient and stoichiometric characteristics among different plants of the littoral zone of TGR. However, as the dominant factor determining plant distribution (Wu et al. 2009), the effects of water level elevation on leaf nitrogen and phosphorus stoichiometry and stoichiometric homeostasis are not clear. In the study, we choose the section from Zhongxian County of Chongqing to Zigui County of Yichang City to carry out a field investigation. This aim of the study was to investigate the effects of water surface elevation on stoichiometric characteristics and homeostasis of leaf nitrogen and phosphorus in hydro-fluctuation zone of the TGR. Furthermore, we tried to explain the distribution and composition of the plant community by plant nitrogen and phosphorus utilization strategy to adapt to changed water surface elevation in the hydro-fluctuating habitat.

Materials and methods

Study sites and field sampling

The section from Zhongxian County of Chongqing (N30°03′–30°35′, E107°32′– E108°14′) to Zigui County of Yichang City (N30°38′–31°11′, E114°18′– E111°0′) is located in the middle and downstream of the TGR from central Chongqing to the west of Hubei Province, with a total length of 419.5 km. The whole investigated area is located in subtropical monsoon humid climate region. In June 2018, a field investigation was carried out regarding nitrogen and phosphorus content of plant leaves and soil located in hydro-fluctuation zone of the section from Zhongxian County of Chongqing to Zigui County of Yichang City, which included six sampling sites. The six sampling sites are Shibao Zhai (N30°23′48″ E108°8′43″), Hanfeng Pool (N31°8′40″ E108°30′36″), Qukou Town (N31°7′26″E108°28′13″), Shuitian Dam (N31°2′52″ E110°41′53″), Wan'gu Temple (N30°1′3″ E110°44′51″), and Xiangxi River (N30°57′60″ E110°45′35″), respectively (Fig. 1). Field habits and work pictures at six sampling sites was shown as Fig. S1 in supplementary materials.

At each survey site, we selected a sampling section with less human interference, similar habitat characteristics, and obvious dominant species. Each section was divided into three water surface elevations (L:145–155 m, M: 155–165 m, H:165–175 m). Three 1 m × 1 m quadrats were set up at each elevation, with a total of 54 quadrats for six sampling sites. In each quadrat, 30–50 fresh, full, and complete leaves of each dominant species were randomly selected. The aboveground biomass was sampled by clipping all plants on the ground within a 1 m × 1 m quadrat, and all the plants were sorted to species and record. Relative biomass of one species was calculated as the ratio of biomass of single species to all species in a quadrat. Community coverage was obtained by visual grid method. At the same time, considering the distribution of plant communities, plant sampling was carried out in 30 m transects on both sides of the quadrat. All plant leaves with good growth in the transect were selected and brought back to the laboratory in dry envelope bags for testing.

For soil sampling, we also divided each sampling sites into three elevations: 145 m–155 m, 155 m–165 m, and 165 m–175 m above the sea level, and took three depths of each quadrat, 0–10 cm, 10 cm–20 cm, and 20 cm–30 cm, respectively. For each depth, we collected 0.2 g soil sample with the soil drilling machine and brought back to the laboratory for measurements.

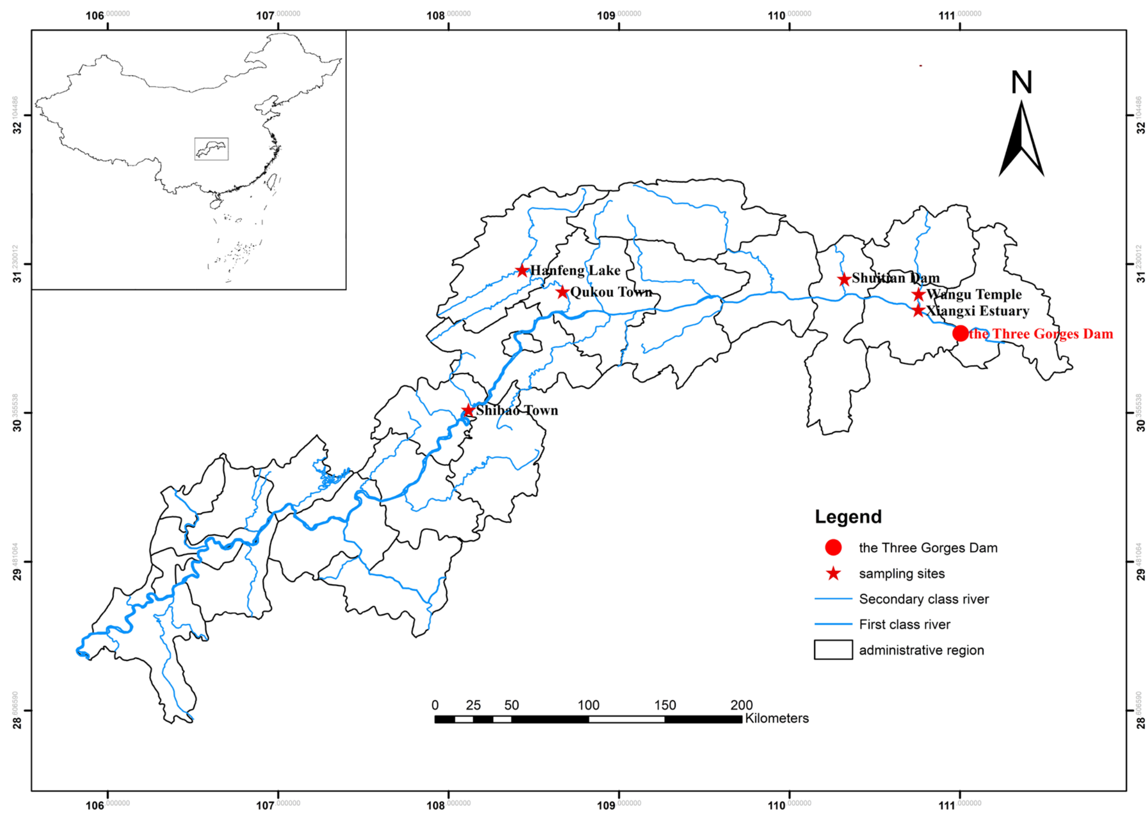

Fig. 1 Locations of six sampling areas in the hydro-fluctuation belt of Three Gorges Reservoir area

Laboratory analysis

After being desiccated at 105 °C for 1 h, plants leaves were dried in a 60 °C oven for 48 h. Then, the leaves were ground with a grass grinder. The semimicro-Kjeldahl method, as described by Bremner (1996), was used to measure the total nitrogen concentration in leaves, using the digestion methods described by Moreno-Alvarado et al. (2017). After digestion according to He et al (2008), we measure the total *P* concentrations in leaves by the molybdate/stannous chloride method, as described by Kuo (1996).

Soil samples collected are dried until they lose moisture and ground through a 1-mm sieve to remove debris. Total *N* concentrations of the soil were also determined by the semimicro-Kjeldahl method (Bremner 1996). While the total phosphorus concentration in soil were determined by anti-spectrophotometry with sodium hydroxide and molybdenum antimony (Kuo 1996).

Calculation and analysis

According to Su et al. (2019), the stoichiometric steady-state H was calculated by the equation:

$$\log(y) = \log(c) + (1/H)\log(x) \quad (1)$$

where *y* is the *N* (or *P*) content of plants, the *x* is the average *N* (or *P*) content of three different soil depths (0–10 cm, 10 cm–20 cm, and 20 cm–30 cm, respectively) and *c* is a constant.

To explore the effect of water-level elevation on plant leaf nutrients, we defined *y* as the average *N* (or *P*) content of plants from different sampling locations with the same water surface elevation, and defined *x* as the average *N* (or *P*) content of the soil from different sampling locations with the same water surface elevation.

We use SPSS software to complete data processing, analysis, and rendering. Community *H* (Com_H) was calculated by the species relative biomass (ratio of biomass of single species to all species) multiplied by species *H* in a quadrat, as follows (Yu et al. 2010; Su et al. 2019):

$$\text{Community }(H) = \sum_{i=1}^{n} \text{relative\_biomass}_i \times H_i$$

where *n* is the total number of plant species in the quadrat, and *i* varies from 1 to *n*. Then, linear regression method was carried out to study the relationship between community coverage and community *H*.

Results

Nitrogen and phosphorus content of the plants with water surface elevation

We took 120 plant samples in the ebb and fall zone of TGR, with 50 plant species included. The nitrogen content of these 120 plant samples ranged from 3.22 mg·g^{-1} to 68.37 mg·g^{-1}, with an average value of 23.71 mg·g^{-1}. The phosphorus content ranged from 0.22 mg·g^{-1} to 13.97 mg·g^{-1}, with an average value of 3.29 mg·g^{-1}. In the water surface elevation 145 m–155 m (L), 155 m–165 m (M), and 165 m–175 m (H), plant tissue N was significantly correlated with plant tissue P, and R^2 values were 0.25 ($p=0.04$), 0.37 ($p<0.001$) and 0.28 ($p<0.001$), respectively. Higher means of N content of plant tissue was found at H section (Fig. 2).

The number of plant species increased with increasing water surface elevation (12 species from 145 m to 155 m, 17 species from 155 m to 165 m, 45 species from 165 m to 175 m). For non-dominant species, the nitrogen content ranged from 8.40 mg·g^{-1} to 68.37 mg·g^{-1}, with the average value of 30.07 mg·g^{-1}. The phosphorus content ranges from 0.22 mg·g^{-1} to 13.97 mg·g^{-1}, with the average value of 4.28 mg·g^{-1}. *Cynodon dactylon* (Linn.) Pers, *Abutilon theophrasti* Medik, *Xanthium sibiricum* Partin ex Wider, and *Bidens pilosa* Linn were all found in three water surface elevations.

For four dominant species, the nitrogen content ranged from 5.22 mg·g^{-1} to 43.18 mg·g^{-1}, with the average value of 19.43 mg·g^{-1}. The phosphorus content ranges from 1.23 mg·g^{-1} to 9.29 mg·g^{-1}, with the average value of 4.29 mg·g^{-1}. The nitrogen and phosphorus content of *X. sibiricum* and *A. theophrasti* slightly increased with the water surface elevation increasing (Fig. 3). For *C. dactylon*, lower phosphorus and higher nitrogen content was found at the water surface elevation 155 m–165 m. For *B. Pilosa*, no significant difference of nitrogen and phosphorus content existed between different elevations.

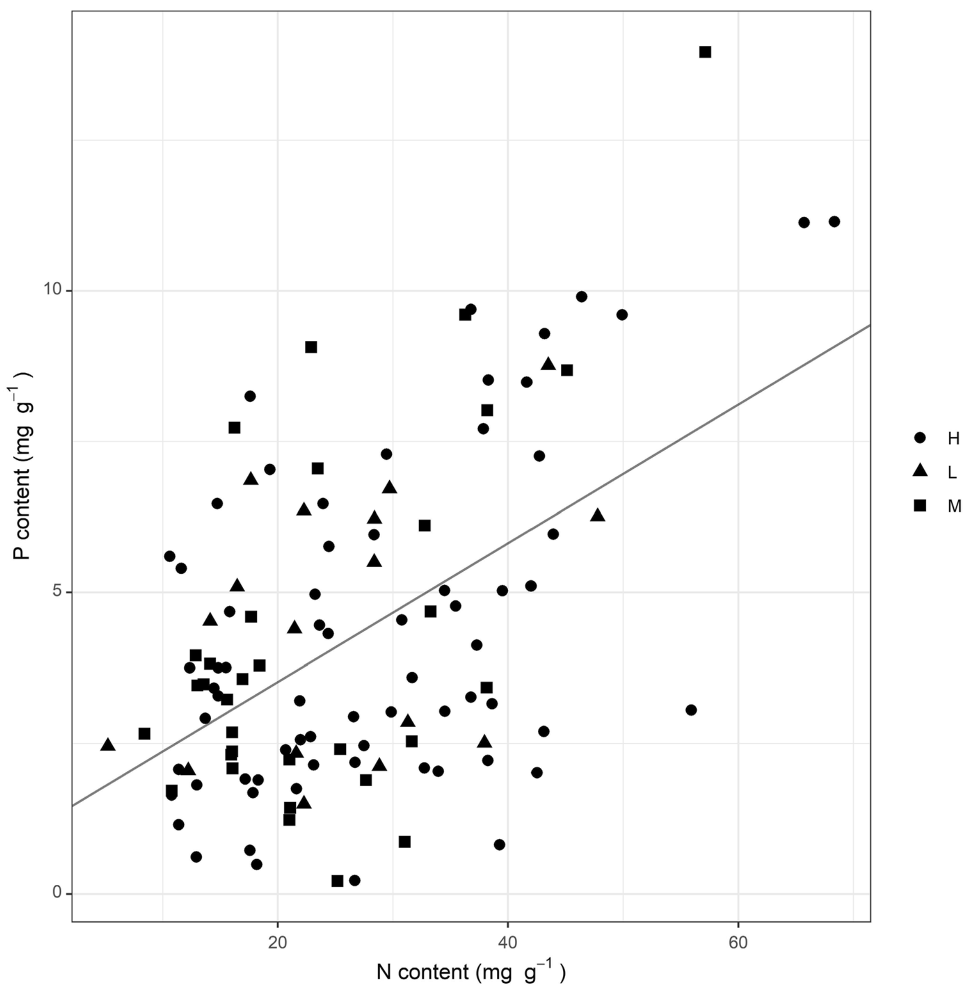

Fig. 2 The relationship between *N* and *P* content of the plants in the hydro-fluctuation zone. *L*, *M* and *H* represented 145–155 m, 155–165 m, and 165–175 m water surface elevation, respectively

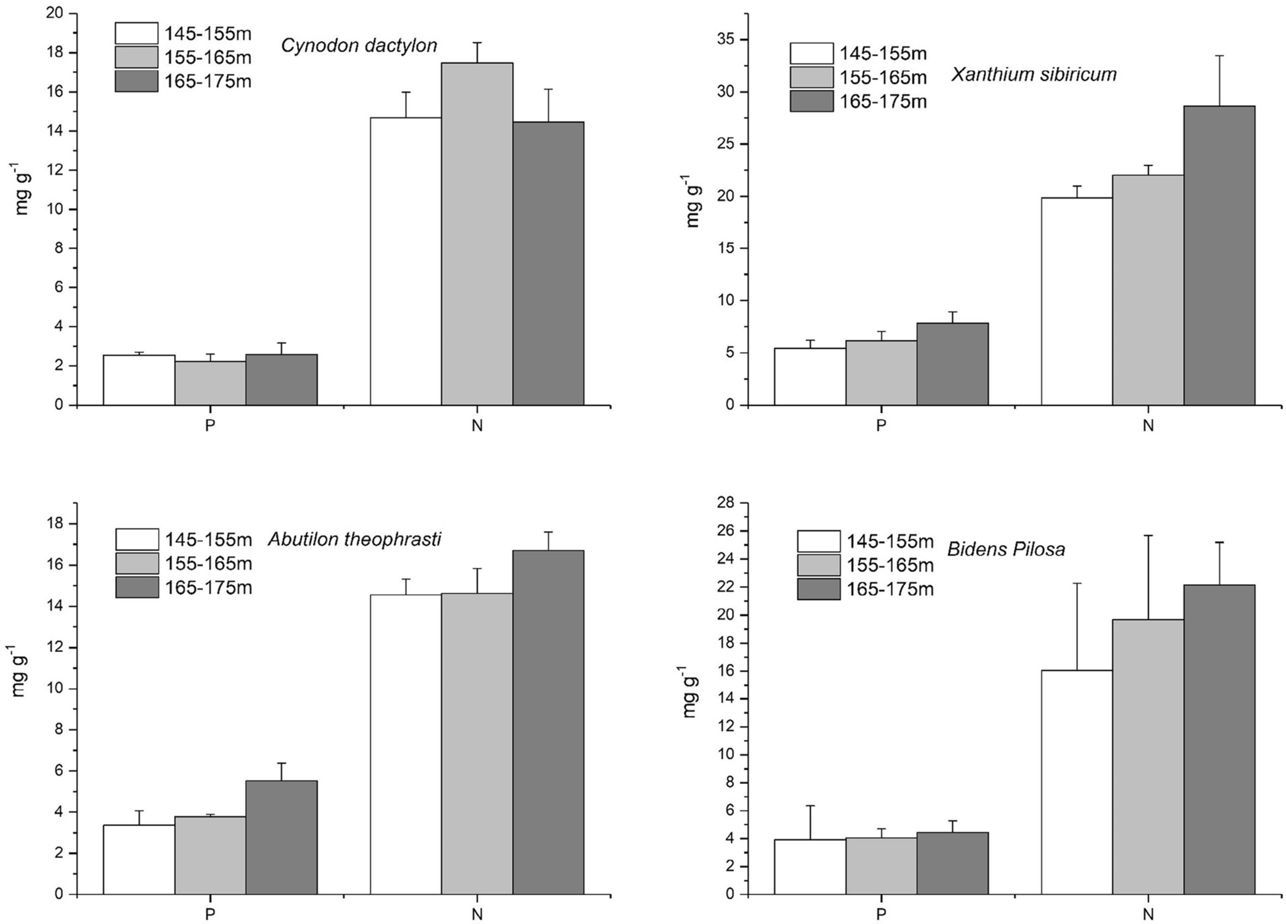

Fig. 3 Nitrogen and phosphorus content (mg·g^{-1}) of four dominant species (*C. dactylon*, *X. sibiricum*, *A. theophrasti*, and *B. pilosa*) at different elevations of the hydro-fluctuation zone

Homeostasis index of nitrogen and phosphorus for dominant species in the hydro-fluctuation zone

The stoichiometric steady-state coefficient of phosphorus (H_P) and nitrogen (H_N) of four dominant species were showed in Figs. 4 and 5.

Along water level elevation, the nitrogen steady-state index (H_N) and the phosphorus steady-state index (H_P) of four dominance species ranged from 1.13 to 5.75 (Fig. 4) and from 1. 40 to 2.24 (Fig. 5), respectively. *X. sibiricum* has the highest value, while *B. pilosa* has the lowest value of H_N and H_P. Persson et al. (2010) pointed out that the H_N (H_P) of a species can vary from below 1.33 to above 4, including four categories. Therefore, *B. pilosa* was plastic for *N* element ($0 < H_N < 1.33$) and weakly plastic for *P* element ($1.33 < H_P < 2$), both *C. dactylon* and *A. theophrasti* were weakly homeostatic for *N* element ($2 < H_N < 4$) and weakly plastic for *P* element ($1.33 < H_P < 2$), while *X. sibiricum* was homeostatic for *N* ($H_N > 4$) and weakly homeostatic ($2 < H_P < 4$) for *P* element.

Relationship between community steady-state index and coverage

The community coverage from six sampling region increased with the elevation of water level. Linear regression revealed the community H_N and H_P were positively correlated with the community coverage (Fig. 6).

Discussion

The effect of water surface elevation on leaf nitrogen and phosphorus stoichiometry

A number of studies have demonstrated that plant *N* and *P* concentrations are significantly affected by temperature and latitude (Reich and Oleksyn 2004; Tang et al. 2018), habitat (Koerselman and Meuleman 1996; Yu et al. 2011), and plant functional type (Yu et al. 2011; Xia et al. 2014). In the present study, the phosphorus content of 120 plant

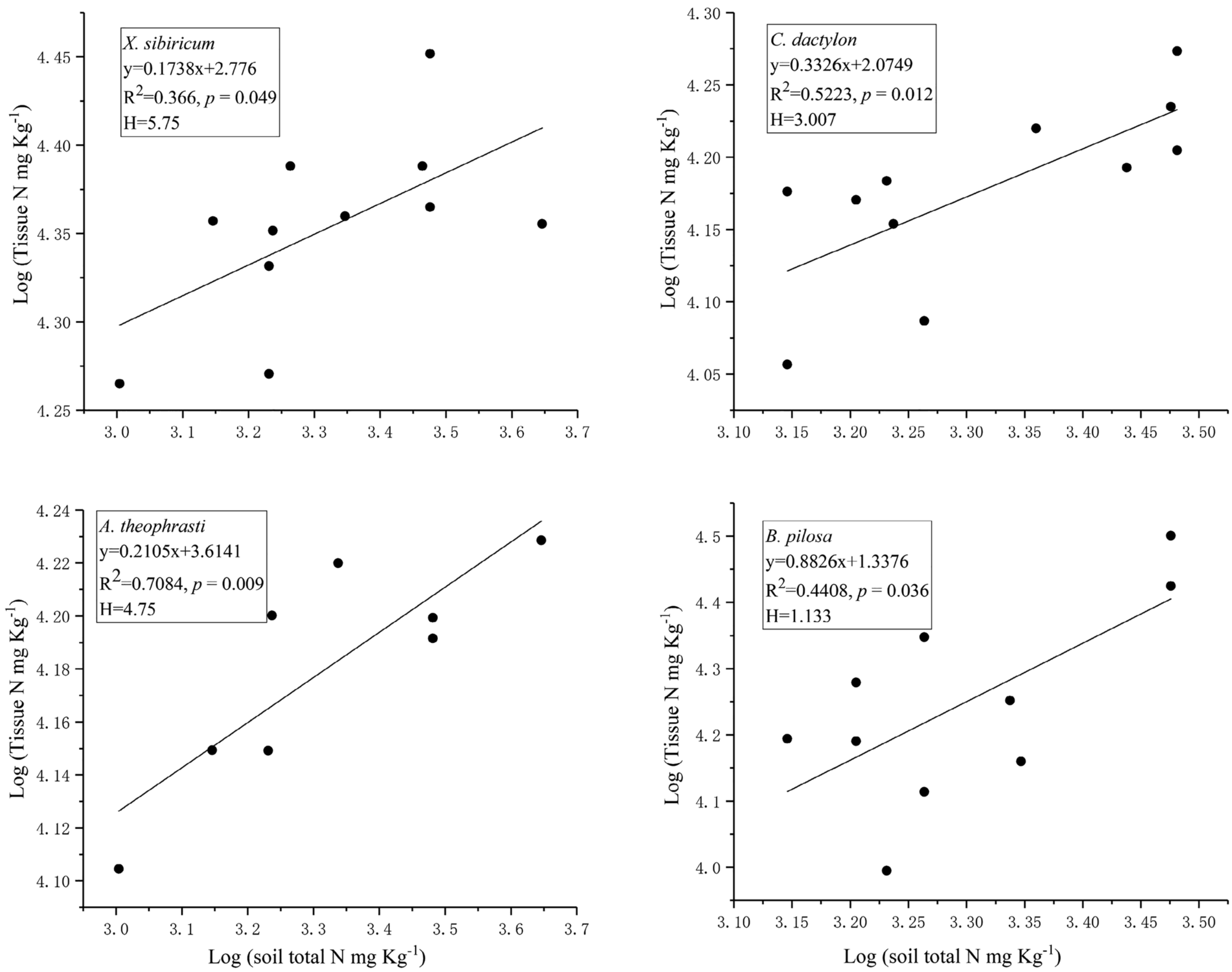

Fig. 4 The relationship between soil total N and plant tissue N of four dominant species. Stoichiometric Homeostasis coefficient (H) was calculated by the equation: log (y) = log (c) + (1/H) log (x), where is the N content of plants, x is the N content of the soil, and c is a constant

samples ranged from 0.22 mg·g^{-1} to 12.97 mg·g^{-1}, with an average of 3.29 mg·g^{-1}, and the nitrogen content ranged from 3.22 mg·g^{-1} to 68.37 mg·g^{-1}, with an average of 23.71 mg·g^{-1}. Obviously, the mean nitrogen and phosphorus content of the plant species in the falling zone was higher than that of the grassland ecosystem (Han et al. 2005) and the global leaf metering model (Reich and Oleksyn 2004), while close to wetland plant (Hu et al. 2014) and aquatic plants of eastern China (Xia et al. 2014). This indicates that plants of hydro-fluctuation zone of TGR (a special wetland type) gradually forms stoichiometric characteristics similar to wetland vegetation and aquatic vegetation in the process of vegetation evolution (Kong et al. 2020). As a kind of wetland ecosystem, plants in the falling zone always face a variety of stress environments (Xu et al 2009), and water level elevation is the dominant factor determining plant distribution (Wu et al 2009) and vegetation restoration (Zhu et al. 2020). And after the impoundment, the number of plant species in the hydro-fluctuation belt of TGR area decreased significantly, with more single genus and single species and the community composition was simplified (Lei et al 2014; Ke et al. 2020). Under the anti-seasonal periodic fluctuation of water level, the life forms of herbaceous plants (including annual and perennial plants) have replaced the life forms of trees, shrubs, and vines as the dominant life forms of plants in the L and M elevations (145 m–165 m) of hydro-fluctuation belt of TGR (Guo et al. 2019; Ke et al. 2020). In the study, the variation of species number and species composition with the elevation (Fig. 2) confirmed it. In an in situ experiment, Li et al. reported that N and P stoichiometry of submerged plants was not directly affected by water level, but by the species itself (Li et al. 2013). Therefore, plant species composition is an important factor affecting stoichiometric characteristics at species level and community level. In the study, the means of N content of four dominant species is lower than that of non-dominant species, and the

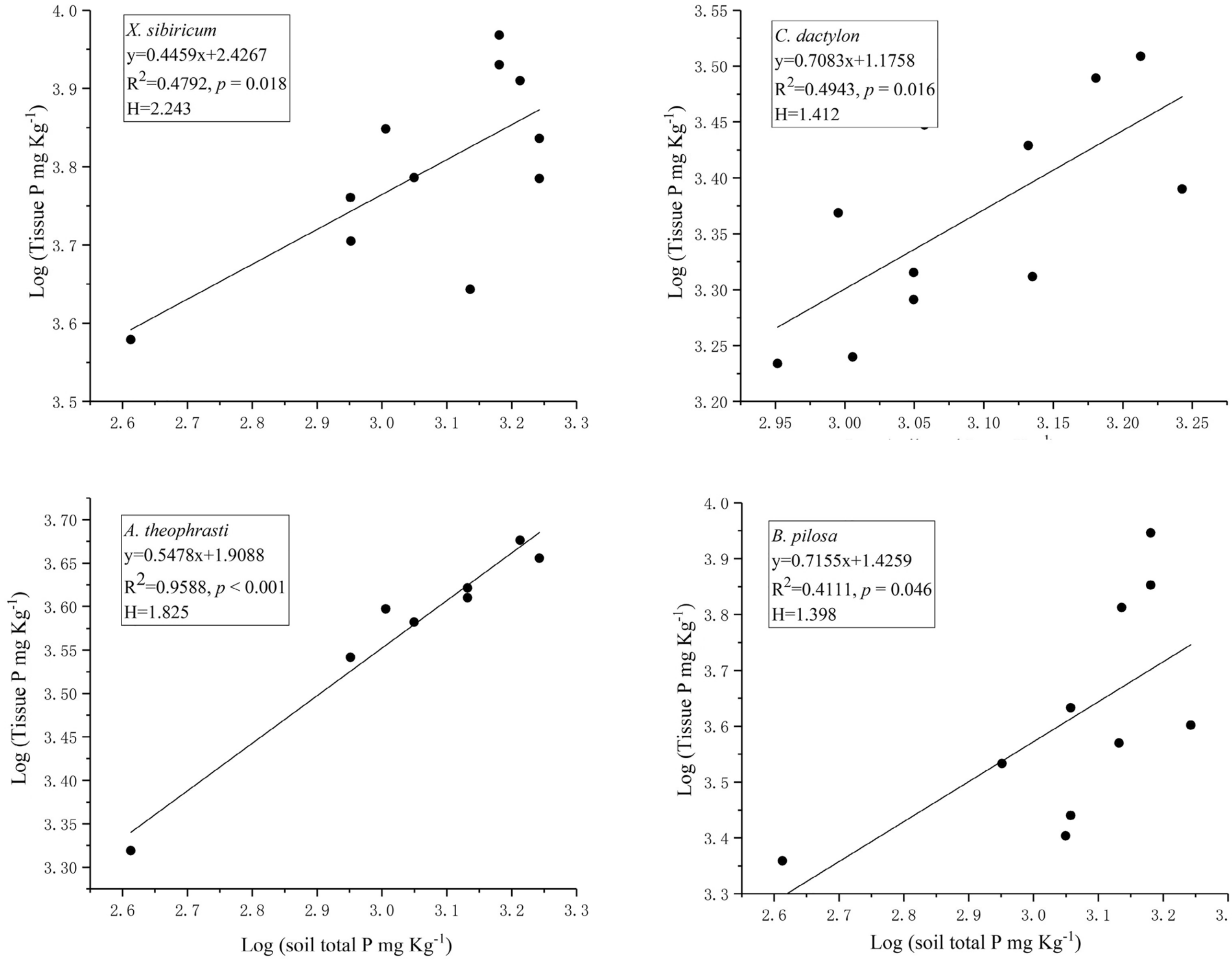

Fig. 5 The relationship between soil total P and plant tissue *P* of four dominant species. Stoichiometric homeostasis coefficient (*H*) was calculated by the equation: log (*y*) = log (*c*) + (1/H) log (*x*), where *y* is the *P* content of plants, *x* is the *P* content of the soil, and *c* is a constant

variation of leaf nitrogen and phosphorus content with elevation existed with specific differences (Fig. 3). As mentioned above, different life forms and species composition existed at different elevations, which resulted in the different stoichiometric characteristics. This could partly explain the higher mean of nitrogen content of the plant species found at the elevation of 165–175 m.

The effect of water surface elevation on stoichiometric homeostasis

The stoichiometric homeostasis H could reflect the ability of plants regulating their element contents in response to nutrient environments changes (Sterner and Elser 2002; Persson et al. 2010; Yu et al. 2010; Golz et al. 2015; Li et al. 2013, 2018). Stoichiometric homeostasis is often element (Li et al. 2013) and species specific (Li et al. 2018). Although there were significant differences in plant nitrogen and phosphorus between sampling sites, the same as reported by Kong et al (2020), and soil nitrogen and phosphorus at six sites also had significant spatial changes, the four dominant plants showed obvious homeostasis and interspecific differences. As showed in Figs. 4 and 5, four dominant species exhibited specific-differences in the phosphorus steady state index (H_P) and nitrogen steady state index (H_N). Although belonging to different categories, both H_P and H_N of four dominant species was in the same order: *X. sibiricum* > *A. theophrasti* > *C. dactylon* > *B. pilosa.* Species with steady-state stoichiometry generally predominate in less nutritional and stable environments (Yu et al. 2010; Li et al. 2018; Su et al. 2019). So, they can be used as an important stoichiometric index to predict the succession of large plant communities and ecosystems responding to varied environmental conditions (Elmqvist et al. 2003; Schefferet al. 2015; Yu et al 2015; Su et al. 2019). In the present study, the H_P and H_N of *X. sibiricum* were higher among the four dominant

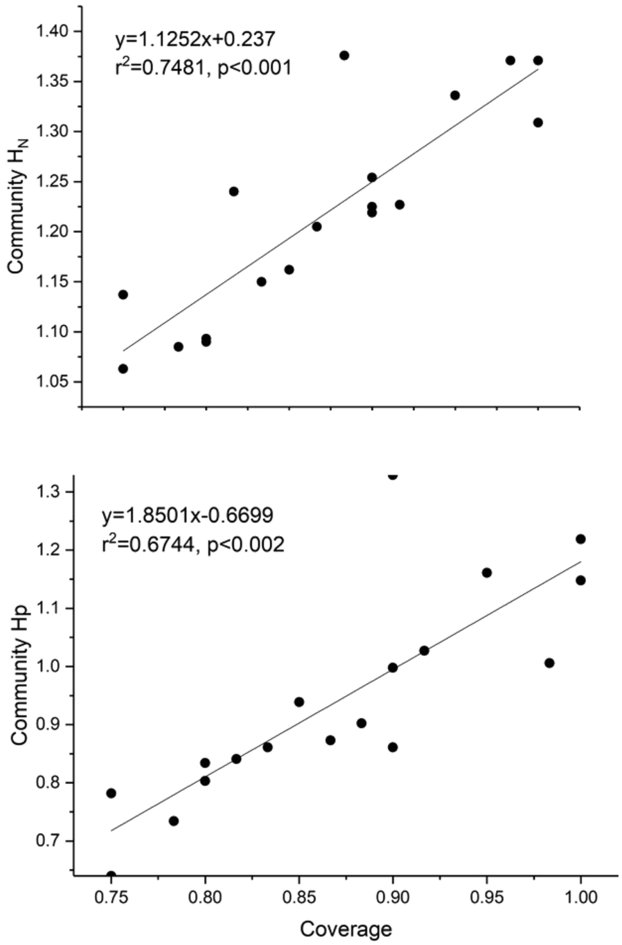

Fig. 6 Relationships between the community coverage and the community H_N and H_P. Both community *H* and coverage were obtained by the means of three quadrat in the same water surface elevation

species, indicating that the *X. sibiricum* were more adaptable, and had higher utilization of nitrogen and phosphorus. However, the first-dominant species in the hydro-fluctuation zone of the section from Zhongxian County of Chongqing to Zigui County of Yichang City of TGR was *C. dactylon* other than *X. sibiricum* (Ke et al. 2020). A possible reason is that *C. dactylon* is a kind of perennial herb with clonal habit, which is vegetatively reproduced by its stolon. And its root system is developed and can adapt to the periodic water level change of TGR better than other species. Community stability positively depended on root biomass (Tilman et al. 2006). Obviously, plants in the falling zone always face periodic water level change. While varied periodic water level change would induce soil stoichiometric imbalance, predominance of high steady state index species would be replaced by low-steady state index species (Su et al. 2019). As reported by Ke et al. (2020), the relative density, relative frequency, and relative coverage of *C. dactylon* in plant community was higher than *X. sibiricum* at three water surface elevations. This can explain the higher dominance of *C. dactylon* compared with *X. sibiricum.*. Furthermore, the water level in the hydro-fluctuation belt of TRG had fluctuated nine times by 2018, but the succession of plant communities needs a long time to occur. The current vegetation is still in the initial stage of renewal and adaptation, and has not reached stability. This may also be one of the reasons for the inconsistency between plant dominance and stoichiometric homeostasis of *C. dactylon* and *X. sibiricum*. For *B. pilosa*, low H_N and H_P indicated low stability but strong plasticity to adapt to the varying external environment. This result was consistent with the reports by Yu et al. (2010, 2011). NO_3^-, as the main soil nitrogen nutrient, is prone to leaching, thus frequent water level fluctuation in the water-fluctuation zone can easily lead to soil nitrogen deficiency. This is why most wetland ecosystems, including the littoral zone of TGR, exhibit nitrogen limitation (Hu et al. 2014; Kong et al. 2020). According to stable leaf nutrient concentration hypothesis (Han et al. 2011), nitrogen is much more stable. This could explain the different categories between H_N and H_P of the same dominant species, for example, both *C. dactylon* and *A. theophrasti* was weakly homeostatic for Nitrogen element and weakly plastic for phosphorus element (Figs. 4, 5).

Relationship between community steady-state index and coverage

As discussed above, the periodic water level variation of TGR changed the plant composition of the hydro-fluctuation belt, and the plant diversity decreased significantly compared with the pre-water storage period (Wang et al. 2011). However, compared with the early flooding period, some plants adapted to the anti-seasonal water level fluctuations and formed new plant communities. And species diversity and coverage have increased (Ke et al. 2020). Due to the different flooding depth and time at different elevations in the hydro-fluctuation belt, there are significant differences in the species composition of plant community at different elevation section (Lei et al 2014). On the one hand, it explains the increase of species number with elevation in this study (Fig. 2), on the other hand, it also explains the change of species stoichiometric characteristics with elevation. As a result, elevation would also affect the coverage and species diversity of plant communities. In the study, increased community coverage with elevation confirmed it (Fig. 6). Species diversity could enhance the resilience of ecosystem states and their ability to stabilize themselves (Elmqvist et al. 2003). It is generally believed that the higher the species diversity index, the more stable the plant community. Investigation on plant community located in the same section reported that species diversity index increased along elevation gradient (Ke et al. 2020). Since community H was calculated as species relative biomass (ratio of biomass of single species to all species) multiplied by species H in a quadrat, the higher community H was found in higher elevation (Fig. 6). In detail, although *X. sibiricum* and *C. dactylon* are dominant species at three elevation, *C. dactylon* and *B. Pilosa* with low H was found more at L and M section, while *X. sibiricum* and *A. theophrasti* with high H were found more at M and H section. This could partly explain the higher community H found at high elevation. Stoichiometric equilibrium had been demonstrated to be associated with species dominance and ecosystem stability (Yu et al. 2010, 2015; Su et al. 2019). In our study, the positive relationship between community steady-state index and community coverage (Fig. 6) partly confirmed it. It maybe suggested that the variation of plant community composition, influenced by anti-seasonal periodic fluctuation of water level, was the determinant factor of stoichiometric homeostasis based on plant community.

Conclusion

In our study, leaf nitrogen content was linearly correlated with leaf phosphorus content along the water surface elevation in the hydro-fluctuating zone of TGR. As the water surface elevation increased, the number of plant species in the fluctuating zone increased. The difference in plant nitrogen and phosphorus steady-state index (H_N and H_P) indicates that there are interspecific differences of nutrient utilization of dominant species and their adaption to water surface elevation. Furthermore, the community coverage increased and the community stability index also increased with water surface elevation. This might indicate that in the fluctuating zone habitat, the plant's nitrogen and phosphorus utilization strategy to adapt to changed water surface elevation affects the distribution and composition of plant community, and ultimately affects the stoichiometric homeostasis on the community levels.

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Author contributions Wang HY wrote the main manuscript text, Sun T carried out the field investigation and experimental measurement, Liu Y and Xiao HL joined in the field investigation, Liu W prepared Figs. 1 and 2. All authors reviewed the manuscript.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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