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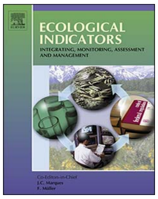

Original Articles

Foliar stoichiometry of carbon, nitrogen, and phosphorus in wetland sedge *Carex brevicuspis* along a small-scale elevation gradient

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ABSTRACT

The concentrations and ratios of plant carbon (C), nitrogen (N), and phosphorus (P) are powerful indicators of various ecological processes. The effect of elevation on the ecological stoichiometric characteristics of plants is presently unclear. Here, we examined the C:N:P ratios of the wetland sedge, *Carex brevicuspis,* along a small-scale elevation gradient and their relationships with the physicochemical characteristics of soil and inundation time of the Dongting Lake wetlands, China. The soil water content and inundation time decreased, whereas the soil bulk density increased with increasing elevation. The height, density, coverage, and aboveground biomass of plants and the organic matter content and total N and P concentrations of the soil increased initially, and then decreased with increasing elevation. The total foliar C concentration and the foliar C:N, C:P, and N:P ratios increased, whereas the total foliar N and P concentrations decreased with increasing elevation. The canonical correspondence analysis (CCA) indicated that the soil water content and inundation time were the primary factors affecting the ecological stoichiometric characteristics of *C. brevicuspis*. The total foliar C concentration and the C:N, C:P, and N:P ratios decreased, but the total foliar N and P concentrations increased with increasing soil water content and inundation time. Our findings highlight the effects of elevation on plant growth and stoichiometric characteristics, which are applicable to the conservation and management of the wetlands dominated with *C. brevicuspis*.

1. Introduction

Ecological stoichiometry mainly focuses on the mass balance of multiple nutrient elements in the ecological systems (Cross et al., 2005; Rong et al., 2015). Plant nitrogen (N) and phosphorus (P) are the most important nutrient elements and the foundation of chemistry composition of living organisms on earth (Elser et al., 2000; Mao et al., 2016). The stoichiometry and relative abundances of carbon (C), N, and P in plants are the powerful indicators of the diverse ecological processes such as population stability, competition, community organization, nutrient limitation, food web, and decomposition (Elser et al., 2000; Güsewell et al., 2003; Yu et al., 2012). Therefore, the studies on plant ecological stoichiometry would enhance our understanding of the growth and nutrient-use strategies of plants, as well as their responses to various environmental stresses.

Nutrient stoichiometry is affected by environmental factors as well as plant physiological processes (Liu et al., 2015). Variations in plant stoichiometry have been documented at different scales, from the molecular and organismal level to the global-scale level (Elser et al., 1996; He et al., 2006; Xia et al., 2014) in different plant functional groups (Wang and Moore, 2014; Zhang et al., 2015), different plant organs of the same species (Li et al., 2014), and in plants growing under various environmental factors such as nutrient, water depth, and light (Cronin and Lodge, 2003; Li et al., 2013a; Xing et al., 2013; Mao et al., 2016).

In freshwater wetlands, the water level plays the most important role in determining plant growth and community structures, and is closely related to the distributing elevations of plants (Deng et al., 2013; Li et al., 2013b). At different distributing elevations in some floodplains and river-connected lakes, a substantial change has been noticed in the soil water content and flooding duration and frequency,

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which in turn, affect the aeration, physical structure, and nutrient availability of soil (Dwire et al., 2006; Anderson and Lockaby, 2011; Deng et al., 2013). Previous studies have extensively investigated the influences of water level on the growth performance, reproduction, and competition in plants (Deegan et al., 2007; Deng et al., 2013; Li et al., 2015). Moreover, a few studies conducted on the forest ecosystems have confirmed that the foliar N and P concentrations can increase, decrease, or remain unchanged along an elevation gradient (Du et al., 2016), while the leaf N:P ratio decreased with increasing elevation (Fisher et al., 2013). However, limited studies have been conducted to investigate the changes in the ecological stoichiometry of plants along an elevation gradient in wetland ecosystems.

Dongting Lake, located in the middle reach of the Yangtze River, is the second largest freshwater and a typical river-connected lake in China (Xie and Chen, 2008). In this lake, *Carex brevicuspis* is one of the dominant sedge species, and is distributed widely at different elevations with various important ecological functions, such as serving as the main food resource for migratory birds and a spawning ground for migratory fish. However, in the recent years, the *C. brevicuspis* community has been seriously degraded because of the changes in hydrological regime caused by intensive anthropogenic disturbances. Therefore, it is an ideal species for investigating the relationship between elevation gradient and plant stoichiometry.

In the present study, we focused on the foliar stoichiometric characteristics (including the total C, N, and P concentrations and the C:N, C:P, and N:P ratios) of the *C. brevicuspis* community along a small-scale elevation gradient in Dongting Lake. We determined the physicochemical characteristics of soil (water content, bulk density, and total N, total P, and organic C concentrations) and inundation time at different elevations. The aims of this study were to examine (1) the difference in growth and foliar stoichiometric characteristics of *C. brevicuspis* at different elevations, and (2) the relationships between plant foliar stoichiometric characteristics and soil physicochemical characteristics and inundation time.

2. Materials and methods

2.1. Study site

Dongting Lake (28°30′–30°20′N, 111°40′–113°10′E) receives inflow mainly from the four rivers (Xiang River, Zi River, Yuan River and Li River) and the four channels (Songzi, Taiping, Ouchi and Tiaoxian) linked to the Yangtze River (Fig. 1). The water level changes significantly with different seasons; the wetlands are usually flooded during May–October and relatively dry during November–April. The mean annual temperature is 16.4–17.0 °C and the average annual precipitation is approximately 1382 mm (Chen et al., 2014).

This study was conducted on the Dingzidi lakeshore (29°25′25.8″N, 112°56′45.8″E) located in East Dongting Lake. *Carex brevicuspis* is distributed widely in this lakeshore from the adjacent areas of the water body to the embankment. On this lakeshore, *C. brevicuspis* forms mono-dominant communities along a mild slope of 5–10°. The elevation ranged from 22.6 to 26.2 m on this lakeshore, making it an ideal site for investigating the stoichiometric characteristics of *C. brevicuspis* at different elevations.

2.2. Study species

Carex brevicuspis is widely distributed in Taiwan and eastern mainland China (Dai et al., 2010). It can form mono-dominant communities or exist co-dominantly with other species, such as *Miscanthus sacchariflorus* and *Polygonum hydropiper*, in Dongting Lake. Depending upon the flooding pattern of Dongting Lake, *C. brevicuspis* usually has two growing seasons; it flowers and fruits in April or May before the flooding begins, and is completely submerged during the flooding season. After flooding, the shoots emerge immediately (November) and keep growing till January. In January, the above-ground plant parts become withered because of the cold temperature. Subsequently, the new ramets emerge and grow rapidly in February or March (Deng et al., 2013).

2.3. Field sampling

In May 2012, the sampling sites were established on the Dingzidi lakeshore before flooding. Seven transects, parallel to the water body and 150 m away from each other, were set up. The first transect was approximately 20 m away from the water body. Nine plots of 1-m^2 area were established in each transect, and the distance between each plot was 50 m. The density, height, and coverage of *C. brevicuspis* shoots were recorded. Plant density was defined as the number of plants in each plot. Plant height was measured using a steel tape with 0.1-cm scale. Additionally, a global positioning system (MG758E; Beijing UniStrong Science & Technology Co., Ltd., Beijing, China) was used to record the geographical coordinates of plants. Because *C. brevicuspis* is a perennial acaulescent herb, it is difficult to distinguish between the dead live roots. Therefore, we chose the leaves of *C. brevicuspis* as our study material. The leaves of the mature plants with similar growth performance were collected from each plot. Mature plant leaves were defined based on the length of leaves. Subsequently, all aboveground parts of the plants were mowed, and stored in the labeled polyethylene bags for measuring their aboveground biomass later.

After examining the vegetation, a 100-cm^3 soil sampler was used to collect the soil samples for measuring the soil bulk density in each plot of 0–20 cm depth. Five such soil samples were collected from each of the four corners and the center of each plot. Subsequently, these five samples were thoroughly mixed into one composite sample for each plot. All plants and soil samples were placed in the labeled polyethylene bags and transported to the laboratory, where they were kept at 4 °C until analysis. The samples were analyzed within less than 20 days.

2.4. Laboratory analysis

All leaf samples were oven-dried to a constant weight at 70 °C, and subsequently ground for further analysis. Total N and C concentrations of leaves were measured by an elemental analyzer (Vario MAX CN, Elementar, Germany), and total P concentration of leaves was measured by molybdenum blue colorimetric method after digesting the leaf samples in a solution of sulfuric acid (H_2SO_4) and hydrogen peroxide (H_2O_2) (Zhang et al., 2015).

The soil samples were air-dried and sieved to remove the coarse fragments (< 0.15 mm for total N, total P and organic C contents; < 0.25 mm for other index analyses). The soil organic C content was measured by the wet oxidation of organic matter with a solution of potassium dichromate (KCr_2O_7) and H_2SO_4, followed by the back titration with ferrous sulfate ($FeSO_4$; Zhang et al., 2015). The samples were then analyzed for the total soil N concentration using Kjeldahl method and for the total soil P concentration using acid digestion with a solution of H_2SO_4 and perchloric acid ($HClO_4$) solution (Zhang et al., 2015). The soil water content was measured by oven-drying method (Zhang et al., 2015). Additionally, using the digital elevation model (1:10,000) of Dongting Lake (Changjiang Water Resources Commission, Ministry of Water Resources, China, 1995) and the coordinates of each plot, their distributing elevations were calculated with an accuracy of 0.1 m. The inundation time was calculated on the basis of the daily water level data (8:00 a.m.) obtained from Chenglingji hydrological gauging station in 2011.

2.5. Data analysis

One-way analysis of variance (ANOVA) was performed in conjunction with Duncan's test to determine the effects of elevation on the stoichiometric characteristics of *C. brevicuspis*. Tukey's test was used for

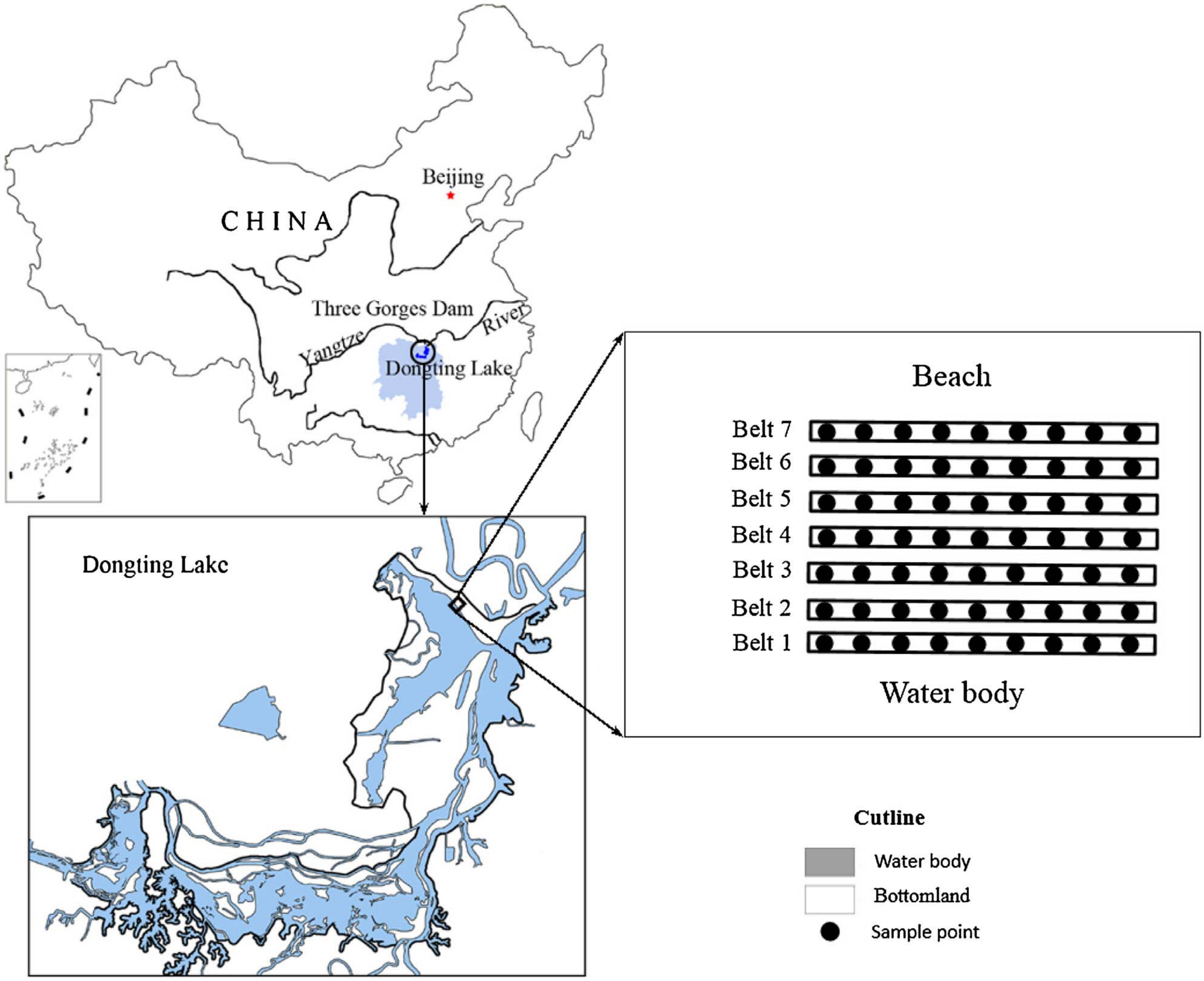

Fig. 1. Water system and location of sampling sites in Dongting Lake. Shaded areas indicate the wetlands.

Table 1
Vegetation characteristics of *Carex brevicuspis* community in different sampling transects along a small-scale elevation gradient. Different letters indicate significant differences among treatments at the 0.05 significance level.

Transects	Height(cm)	Density (m^{-2})	Coverage(%)	Above ground biomass ($g\ m^{-2}$)
1	39.2 ± 3.8a	844.9 ± 135.3b	76.1 ± 6.8b	309.7 ± 42.3a
2	71.2 ± 2.8b	1157.3 ± 81.9bc	91.1 ± 2.3c	584.5 ± 38.4bcd
3	75.9 ± 3.5b	1589.3 ± 136.6d	94.5 ± 4.5c	602.7 ± 44.0 cd
4	72.2 ± 2.7b	1207.1 ± 158.7c	93.3 ± 2.8c	487.4 ± 48.9bc
5	76.4 ± 5.7b	1212.4 ± 50.9c	94.4 ± 2.1c	623.6 ± 45.5d
6	71.1 ± 2.5b	981.6 ± 83.5bc	82.2 ± 3.2bc	451.2 ± 23.5b
7	45.4 ± 5.5a	523.3 ± 66.6a	51.7 ± 6.9a	286.8 ± 64.9a

the multiple comparisons. In order to reduce the heterogeneity of variances, the data were log10-transformed, if necessary. Liljefor's and Levene's tests were used to test the normality and homogeneity of data, respectively.

Canonical correspondence analysis (CCA) was used to analyze the relationships between the vegetation stoichiometric characteristics of *C. brevicuspis* and sediment properties and inundation time of Dongting Lake. The vegetation data matrix included the stoichiometric characteristics of *C. brevicuspis*, and the environmental data matrix consisted of the soil properties (water content, bulk density, and total N, P, and organic C concentrations) and inundation time. The CCA was performed using CANOCO v. 4.5 (Plant Research International, Wageningen, Netherlands). The ordination diagrams for plant stoichiometric characteristics and soil properties were analyzed using CanoDraw LITE in order to illustrate the results (Šmilauer, 1992). The relationships between the plant stoichiometric characteristics and soil properties and inundation time were fitted using the SPSS 19.0 software. Moreover, we used the curve estimation for selecting the "best fit" (the highest R^2 and the lowest P-value) relationship for each statistical analysis.

3. Results

3.1. Vegetation and soil characteristics with increases of elevation

Plant height, density, coverage, and aboveground biomass displayed

Table 2
Physicochemical characteristics of soil in different sampling transects along a small-scale elevation gradient. Different letters indicate significant differences among treatments at the 0.05 significance level.

Belts	Water content (%)	Bulk density (g·cm^{-3})	Soil organic carbon (‰)	Total nitrogen (‰)	Total phosphorus (‰)	Elevation (m)	Inundation time (d)
1	40.79 ± 2.92c	1.23 ± 0.03ab	21.13 ± 1.75b	1.80 ± 0.18ab	0.99 ± 0.02c	23.09 ± 0.09a	217.89 ± 1.38f
2	41.42 ± 1.22c	1.19 ± 0.02ab	25.10 ± 2.70bc	2.06 ± 0.17bc	0.86 ± 0.02b	23.86 ± 0.20b	208.11 ± 2.49e
3	36.84 ± 1.52bc	1.20 ± 0.06ab	25.17 ± 1.23bc	2.07 ± 0.13bc	0.89 ± 0.02b	24.77 ± 0.02c	194.33 ± 0.65d
4	37.44 ± 1.40bc	1.13 ± 0.05a	27.52 ± 1.53c	2.38 ± 0.13 cd	0.82 ± 0.06b	25.12 ± 0.04d	186.00 ± 1.01c
5	34.29 ± 0.72b	1.22 ± 0.03ab	27.47 ± 0.64c	2.37 ± 0.06 cd	0.69 ± 0.03a	25.42 ± 0.01e	177.89 ± 0.68b
6	33.77 ± 0.71b	1.28 ± 0.03b	27.89 ± 0.68c	2.54 ± 0.09d	0.79 ± 0.01b	25.89 ± 0.03f	159.22 ± 0.80a
7	23.24 ± 1.00a	1.40 ± 0.04c	14.72 ± 1.39a	1.57 ± 0.12a	0.87 ± 0.02b	26.08 ± 0.02f	156.22 ± 0.15a

similar patterns, which increased initially, and then decreased with increasing elevation (Table 1). The soil water content and inundation time decreased, while the soil bulk density increased with an increase in elevation (Table 2). The total soil organic C, N, and P concentrations displayed similar patterns, which increased initially, and then decreased with increasing elevation (Table 2).

3.2. Foliar C, N, and P concentrations with increases of elevation

The total foliar C concentration of *C. brevicuspis* increased significantly with increasing elevation ($F = 14.183$; $df = 8$; $P < 0.05$; Fig. 2). The highest total foliar C concentration (transect 7; 410.8 ± 2.0 mg g^{-1}) was present in the highest elevation transect, which was 1.1-fold higher than the lowest total foliar C concentration (383.4 ± 4.0 mg g^{-1}) present in transect 2, close to the water body. The total foliar N concentration, ranging from 15.4 mg g^{-1} to 16.7 mg g^{-1}, decreased with increasing elevation ($F = 2.754$; $df = 8$; $P < 0.05$; Fig. 2). The total foliar P concentration displayed a pattern similar to that of total foliar N ($F = 14.086$; $df = 8$; $P < 0.05$; Fig. 2). The highest total foliar P concentration (1.1 ± 0.0 mg g^{-1}) was

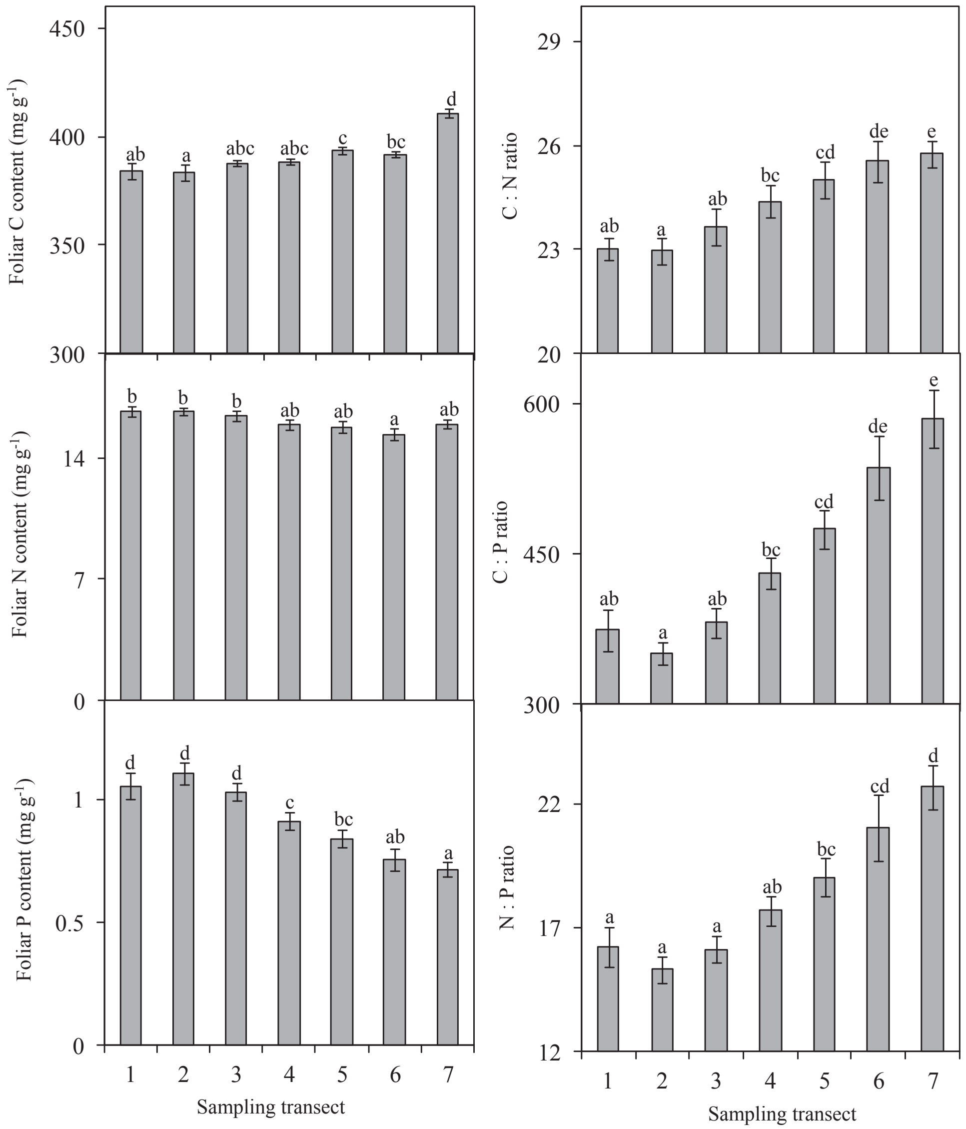

Fig. 2. Stoichiometric characteristics of *Carex brevicuspis* (means ± standard error; n = 9) at different sampling transects along a small-scale elevation gradient. Different letters indicate significant differences among treatments at the 0.05 significance level.

Table 3
Summary of the canonical correspondence analysis (CCA) ordinations.

Environmental factors	Axis 1	Axis 2
Water content	**−0.5112**	−0.0769
Soil bulk density	0.1945	0.1035
Soil organic C content	−0.0713	−0.0012
Soil total N content	0.0959	−0.0193
Soil total P content	−0.2244	**−0.3086**
Inundation time	**−0.7480**	−0.0560
Eigenvalues	0.006	0.000
Species-environment correlations	0.764	0.368
Cumulative percentage variance of species data (%)	57.3	57.5
Cumulative percentage variance of species-environment relation data (%)	99.6	99.9

$P < 0.05$

present in transect 2, which was 1.5-fold higher than the lowest one present in transect 7 (0.7 ± 0.0 mg g^{-1}).

3.3. Foliar C:N, C:P and N:P ratios with increases of elevation

The foliar C:N, C:P, and N:P ratios displayed similar patterns, all of which increased significantly with increasing elevation. The highest foliar C:N, C:P, and N:P ratios (25.8 ± 0.4; 584.8 ± 28.9; and 22.7 ± 0.9, respectively) present in belt 7 were respectively 1.1-, 1.7-, and 1.5-fold higher than the lowest foliar C:N, C:P, and N:P ratios (23.0 ± 0.4; 350.4 ± 10.8; and 15.3 ± 0.5, respectively) present in belt 2 (Fig. 2).

3.4. Correlation analysis

The first and second axes of the CCA ordination explained 99.6 and 99.9% of the total variance of species-environment relationship, respectively (Table 3; Fig. 3). The first axis was negatively correlated with the soil water content and inundation time. The second axis was negatively correlated with the total soil P content.

The total foliar C content and the foliar C:N, C:P, and N:P ratios decreased, but the total foliar N and P concentrations increased significantly along with increasing soil water content and inundation time (Figs. 4 and 5).

4. Discussion

In wetlands, elevation is one of the most important factors for determining the microsite conditions that affect the growth and physiology of a plant species. Our results indicated that the total foliar C content increased, while the total foliar N and P contents decreased along with the increasing elevation, suggesting that elevation had a significant effect on the concentrations of nutrient elements. The contrasting values of the total foliar C, N, and P contents in response to changes in elevation might be accounted for by the dilution effect (Li et al., 2013a). A rapidly growing plant might allocate more N and P to the photosynthetic tissues for supporting high CO_2 assimilation; a dilution effect of the higher C-gain of the plant decreases its total N and P concentrations (Yan et al., 2006; Li et al., 2013a).

The N:P ratio, rather than the individual concentrations of N and P, plays a more important role in assessing the nutrient limitation of plants (Koerselman and Meuleman, 1996; Güsewell and Koerselman, 2002). Our results showed that *C. brevicuspis* had an N:P ratio > 16 at most of the elevations, indicating that the growth of *C. brevicuspis* was limited by P based on the criterion proposed by Koerselman and Meuleman (1996). Phosphorus is generally considered as the most limiting nutrient in freshwater wetland systems, especially for tropical and subtropical wetlands (Bedford et al., 1999). Other studies have also reported that the subtropical soils are generally deficient in P (Tian et al., 2010). In Dongting Lake, the long-term inundation would produce the long-term anaerobic conditions, which can increase the solubility and mobilization of iron from soils. This, coupled with regular flushing,

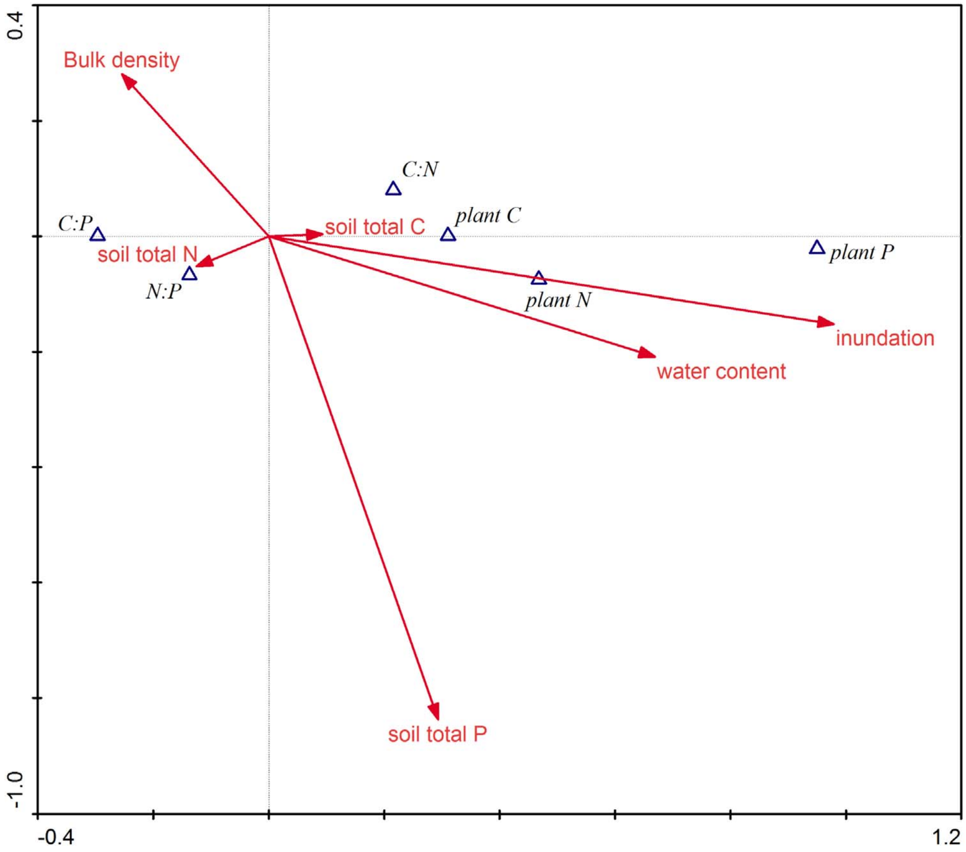

Fig. 3. Canonical correspondence analysis (CCA) ordination for the foliar stoichiometric indices and soil environmental characteristics and inundation time of *Carex brevicuspis* communities. C: plant C content; N: plant N content; P: plant P content; C:P: ratio of the plant C and P contents; C:N: ratio of the plant C and N contents; N:P: ratio of the plant N and P contents; TC: soil organic C content; WC: soil water content; TN: total soil N content; TP: total soil P content; IT: inundation time; SBD: soil bulk density.

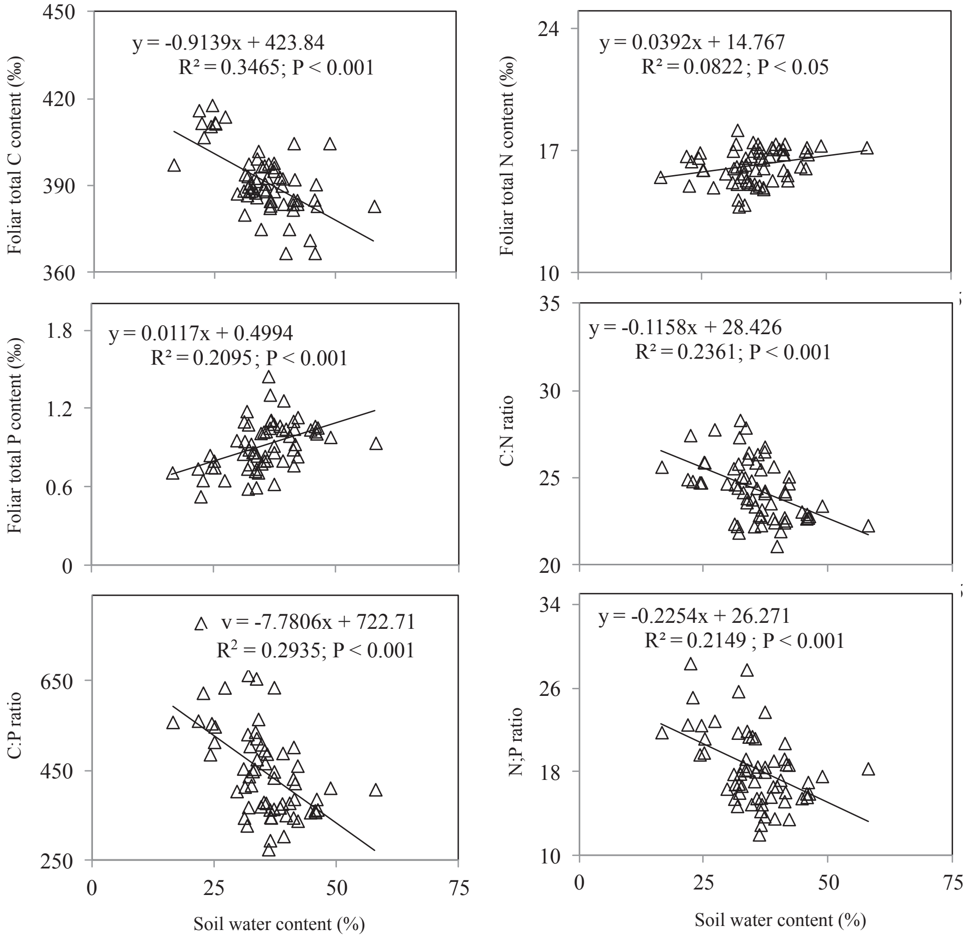

Fig. 4. Relationship between the foliar stoichiometric characteristics and soil water content of *Carex brevicuspis* at different sampling transects along a small-scale elevation gradient.

might explain the limitations of P in the *C. brevicuspis* community (Anderson and Lockaby, 2011). Moreover, a plant regulates its N content more than its P content (Aerts and Chapin, 2000), which, in turn, is more dependent on the nutrient availability than the N content, which might be another possible explanation for the limited P content (González et al., 2010).

Soil nutrients are the primary source of plant nutrients; therefore, the soil N and P concentrations should determine the plant N and P concentrations (Chen et al., 2013; Li et al., 2014). However, our CCA results indicated that the soil water content and inundation time, rather than the soil nutrient contents, played a more important role in determining the stoichiometric characteristics of *C. brevicuspis*. This was also confirmed by our correlation analysis between the foliar stoichiometric characteristics and the soil water content and inundation time. Water regimes, such as flood duration and frequency, affect nutrient transformation and availability by controlling various biogeochemical processes (Anderson and Lockaby, 2010), rather than determining plant stoichiometric characteristics. In this study, the total foliar C content and the foliar C:N, C:P, and N:P ratios decreased along with increasing soil water content and inundation time. This result is in contrast with the findings of Liao et al. (2013), which reported that the C:N and C:P ratios of *Calamagrostis angustifola* increased with an increase in soil moisture. At a global scale, Ordoñez et al. (2009) reported that the soil moisture had no influence on the N concentration of leaves. These results suggested that the influence of water conditions on plant stoichiometry differed significantly with ecosystem types and plants. Plant growth and photosynthesis would be limited in relatively high soil water conditions, which might be the main reason for the reduction of the total C content and C:N and C:P ratios along with increasing soil water content and inundation time. However, we did not test the photosynthetic traits of *C. brevicuspis* among different elevations in this study. Moreover, the nutrient concentrations and N:P ratio in the vegetation were poorly correlated with various measures of soil nutrient availability (Güsewell and Koerselman, 2002). One possible reason for this poor relationship might be the well-developed root system, which enables the *C. brevicuspis* plant to absorb enough nutrients for its growth (Chen et al., 2014). Another possible reason might be the buffering effect of the belowground nutrient storage in plants, as reported by Bowman et al. (2003).

In conclusion, our results indicated that the soil water content and inundation time induced by different elevations, rather than the soil nutrient status, affected plant growth and ecological stoichiometric characteristics. Recently, the area of *C. brevicuspis* community in Dongting Lake was seriously reduced because of the reduced water levels and anthropogenic disturbances (e.g., fire, wheat planting, and grazing). Therefore, understanding plant growth and ecological stoichiometric characteristics at various elevation conditions would not only contribute to our understanding of many ecological processes (e.g. biogeochemical cycles, carbon sequestration), but also contribute to the establishment of the effective measures for plant protection and biodiversity maintenance.

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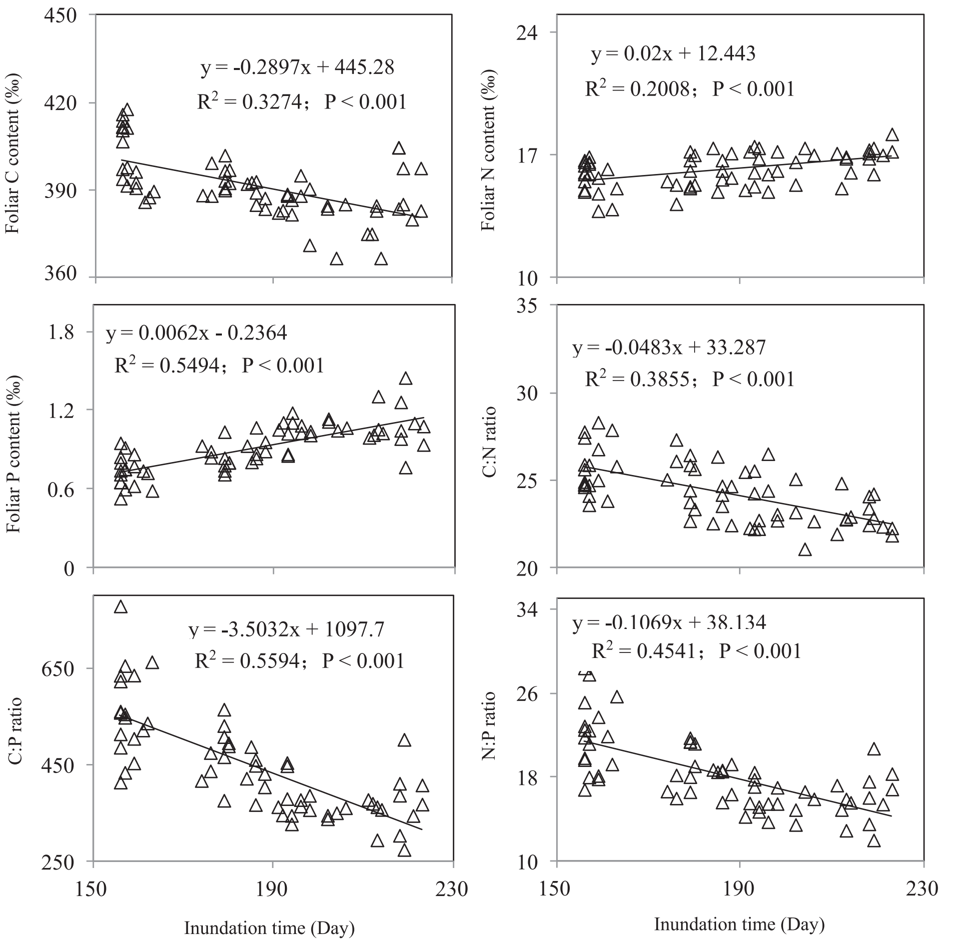

Fig. 5. Relationship between the foliar stoichiometric characteristics and elevation of *Carex brevicuspis* at different sampling transects along a small-scale elevation gradient.

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