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Hydrologic-induced concentrated soil nutrients and improved plant growth increased carbon storage in a floodplain wetland over wet-dry alternating zones

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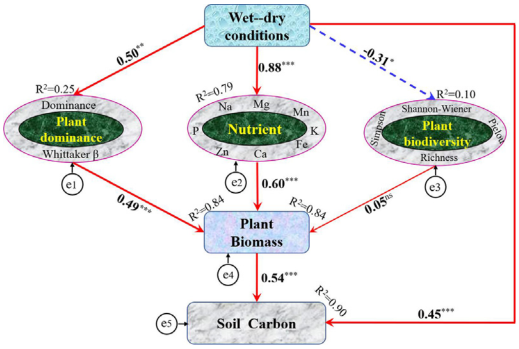
HIGHLIGHTS

- Hydrologically induced concentrated nutrients increased carbon storage over wet-dry alternating zones in a floodplain wetland
- Hydrological gradient variations significantly promote plant growth and carbon sequestration in wetlands by regulating nutrient concentrations
- Hydrological gradient variations in wetlands regulate plant dominance and significantly enhance carbon sequestration

GRAPHICAL ABSTRACT



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ABSTRACT

Hydrological gradient variations in wetlands have a vital impact on wetland carbon storage. However, the mechanisms by which hydrological gradient variations affect biomass and carbon storage by regulating the soil nutrient contents and plant diversity remain unclear. This study attempted to explore these influencing mechanisms by studying the relationships between hydrological gradient variations and carbon storage in wetlands. The results showed that the average nutrient content, plant biomass and soil carbon content values in the high-frequency wet-dry alternating zones (HFWA, zones where the frequency of water level occurs between −25 cm and 25 cm greater than 0.5) were 1.4 times, 2.3 times and 0.43 higher, respectively, than those in the low-frequency wet-dry alternating zones (LFWA, zones where the frequency of water level occurs between −25 cm and 25 cm less than 0.3). These results indicated that the HFWA zones had higher soil nutrients, higher plant dominance, higher biomass and higher soil carbon contents than the LFWA zones. The structural equation model revealed a significant positive correlation between wet-dry alternations and the soil nutrient-plant biomass-soil carbon relation in wetlands. Moreover, there was also a significant positive correlation between wet-dry alternations and the plant dominance-plant biomass-soil carbon relation in wetlands. This implied that the concentrated effect of HFWA on soil nutrients promotes plant growth, enhances plant dominance, promotes plant productivity, and enhances the capacities of plants to input carbon to the soil, thereby increasing the soil carbon content. This study closely linked wetland hydrological gradients, plant biodiversity and wetland

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carbon sequestration and profoundly revealed the mechanisms by which hydrological gradients in wetlands regulate the concentrations of nutrient elements, thereby affecting vegetation growth and carbon sequestration; these results could provide a new cognitive basis for understanding the coupling of carbon and water.

1. Introduction

Wetland ecosystems are a critical and responsive component of the global carbon cycle and play a pivotal role in global carbon storage (Kirschke et al., 2013; Mitsch and Mander, 2018). The carbon content of wetland soils is estimated to account for 20% to 30% of the total global soil carbon content (Rattan, 2008; Mitsch et al., 2013). In the context of the increasing concentration of carbon dioxide in the atmosphere, the carbon sink function of wetlands is extremely important (Moomaw et al., 2018; Wang et al., 2021). Whether a wetland becomes a carbon sink or a carbon source mainly depends on the balance among carbon fixation, carbon storage and carbon release (Kayranli et al., 2010; Nahlik and Fennessy, 2016). Therefore, studying the carbon sequestration effect of wetlands and its influence mechanism is very important. While many studies have focused on the effects of global changes, atmospheric nitrogen depositions, plant community distributions, litter amounts and decomposition rates on carbon sequestration in wetlands (Bernal and Mitsch, 2012; Mitsch et al., 2013; Utstøl-Klein et al., 2015; Zhang et al., 2016), thereby providing a basis on which the carbon sequestration mechanism of wetlands can be understood, few researchers have focused on the impact of hydrological gradients on carbon sequestration in wetlands.

As the main primary producers of wetlands, plants can fix CO_2 in the atmosphere through photosynthesis to form plant organisms (Chapin and V. P.M, 2011; Zhou et al., 2017). They are one of the main sources of carbon accumulation in wetlands and play an important role in carbon storage and carbon sequestration (Villa and Mitsch, 2014). Under different hydrological environmental gradients, the growth process, biomass accumulation and carbon sequestration functions of wetland plants may be very different (Liu et al., 2015). The hydrological processes that occur in wetlands, especially the frequency and duration of wet-dry alternations in wetlands, critically impact the colonization and expansion of plant species, plant biodiversity and the dominance of primary productivity and biomass distributions (Fan et al., 2017; Sardans et al., 2017; Carlson et al., 2020). For example, the highest and lowest water levels that occur in a wetland affect the habitat range of the corresponding plant community and determine the width of the plant community (Shipley et al., 1991). Second, seasonal fluctuations in hydrological processes and the coupling of these processes with local climate cycles affect the germination, growth and reproduction processes of plants (Palanisamy and Chui, 2013; Fu et al., 2018). In addition, the annual average water level also affects the location distribution and species composition of the plant community in a wetland (Luo et al., 2016; Damgaard et al., 2017; Qi et al., 2021). However, do the changes in plant biodiversity and dominance caused by hydrological gradients in wetlands impact plant biomass and soil carbon? This question still lacks an objective answer.

Wetland soil is an important place for global carbon storage, and the carbon cycle process of wetland ecosystem plays an important role in indicating global change (Lal, 2004; Lorenz and Lal, 2018). The hydrological processes that occur in wetlands have an important impact on the soil nutrient and carbon contents in wetlands (Feng et al., 2020). Wetland hydrological processes alter the contents of organic carbon and other nutrients in soils by controlling the retention of nutrients, the accumulation of organic matter and the mineralization of microorganisms (Noe et al., 2012; Marcé et al., 2018). For example, in nutrient-rich floodwaters flow slowly with shallow water depths and a long residence time, the conditions are beneficial for the dissolved nutrients to fully contact the biochemical reaction matrix, and hydrological, chemical and biological retention of the nutrients occurs; thus, nutrients tend to accumulate in the flooded zone (Bernal et al., 2013; García et al., 2017). However, our understanding of how soil nutrients accumulate under different hydrological gradients and how these differences affect the productivity of plants and the soil carbon content in wetlands still lacks profundity.

In wetland ecosystems, the three main components of hydrology, plants and soil, do not exist in isolation but instead interact and act together (Noe et al., 2012; Feng et al., 2020). The hydrological processes that occur in wetlands regulate the migration and enrichment of soil nutrients (García et al., 2017) and affect changes in plant diversity and species dominance (Silvertown et al., 1999; Luo et al., 2016). At the same time, the nutrient contents of wetland soils also affect the germination, growth, reproduction processes and biodiversity of plants (Stevens et al., 2010; Ceulemans et al., 2013; Carlson et al., 2020). Wetland plants can also, in turn, affect the soil nutrient and soil carbon contents through mechanisms such as organic matter inputs (Lange et al., 2015). In short, hydrological processes, plant communities and soil nutrients comprehensively impact carbon fixation in wetlands (Zhang et al., 2002). However, this comprehensive impact is often ignored, and the impact mechanism lacks clarity, causing great uncertainty in understanding the role of wetlands in the global carbon cycle.

Therefore, this study monitored the daily water level, plant biodiversity and dominance, aboveground and underground biomasses, nutrient contents, and soil carbon content along different hydrological gradients on a wetland beach at a Ramsar site (Poyang Lake, the largest freshwater lake in China, site numbers: 2431 and 550) and analyzed the relationships among these factors to reveal the process mechanisms of hydrological gradients on nutrient-plant biomass-soil carbon, plant dominance-plant biomass and soil carbon storage. This study could provide a new cognitive basis for understanding the coupling mechanism of carbon and water, and have strong implication for the verification of global wetland carbon sources / sinks, which can provide a certain scientific basis for achieving global carbon peaking and carbon neutrality goals.

2. Materials and methods

2.1. Study area

The Poyang Lake Wetland (28°22′–29°45′N, 115°47′–116°45′E) is located in the middle of the Yangtze River basin in northern Jiangxi Province, China. The lake catchment has a subtropical warm and wet monsoon climate with an annual mean precipitation of 1680 mm, mainly falling between April and June. This study was conducted at Fengwei Lake, one of the core sublakes in the Nanji Wetland National Nature Reserve of Poyang Lake (Fig. 1); the southern part of the main area of Poyang Lake was newly designated as a Ramsar site in 2020. In this reserve area, obvious flood seasons and dry seasons correspond to the seasonal hydrological regime of Poyang Lake, and the entire area except for Nanshan Island and Jishan Island (with a total area of ≤ 4 km^2) is flooded during the flood season (April to September) in a typical lacustrine hydrological state. However, during the dry season (October of a given year to March of the following year), the lake water recedes into the river courses and some dish-shaped depressions, after which beaches emerge one after another at different elevations, and large and small rivers and dish-shaped lakes are scattered in the area. The entire delta area presents an interlaced landscape of rivers, lakes and islands. This unique hydrological regime, which alternates from the flood season to the dry season within each year, has led to the formation of a large amount of fertile soil, abundant hydrothermal conditions, and the development of a very complex floristic composition of wetland and aquatic plants with extremely high overall productivity.

2.2. Sampling design

Based on our previous long-term monitoring project, we established a 600-m-long and 20-meter-wide transect along an elevational and hydrological gradient from highlands to lowlands on the Fengwei Lake beach. The

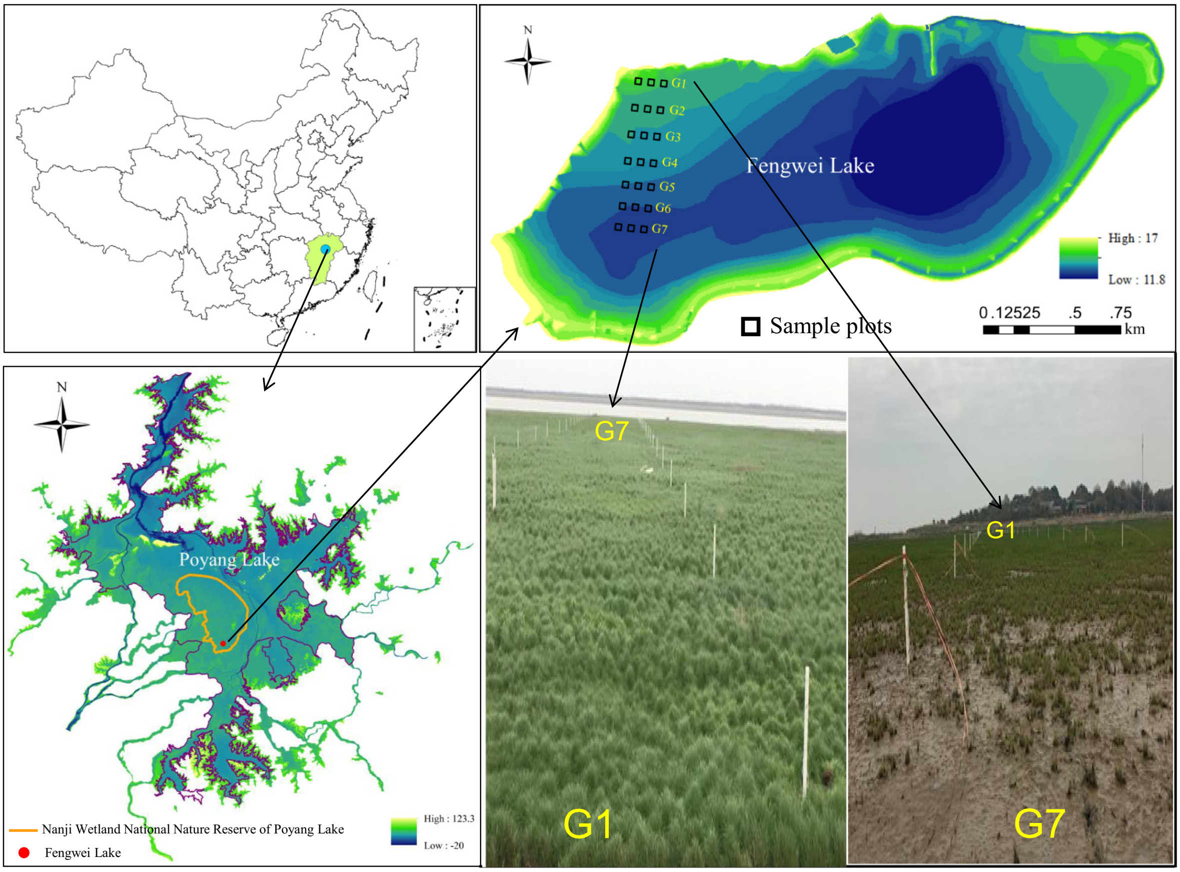

Fig. 1. Schematic diagram of sample plots along a hydrological gradient.

transect started from the lakeshore highlands and passed through the lowland beach before reaching the center of the water body; 56 white polyvinyl chloride (PVC) pipes were used to mark the transect (Fig. 1). A total of 7 gradients denoted G1, G2, G3, G4, G5, G6, and G7 were spanned by this large transect according to elevation and hydrological changes; the G1 gradient was the closest to the lakeshore highlands, while the G7 gradient was the closest to the lake center (Fig. 2).

The distance between each gradient was approximately 100 m. Three 1-m × 1-m plots were selected on each gradient and placed as 3 repeated squares on the gradient, and a total of 21 plots were selected for the investigation and sampling of plant communities and soil. The groundwater level and flooding depth were monitored at each gradient using HOBO U20 data logger automatic water level gauges. In the water level data, negative numbers indicate the groundwater table, and positive numbers indicate the flooding depth. We grouped the 7 gradients into high-frequency dry-wet alternating zones (with an alternating frequency greater than 0.5, including the G4 and G5 gradients, abbreviated as HFWA), medium-frequency dry-wet alternating zones (with an alternating frequency among 0.3 and 0.5, including the G2, G3 and G6 gradients, abbreviated as MFWA),and low-frequency dry-wet alternating zones (with an alternating frequency less than 0.3, including the G1 and G7 gradients, abbreviated as LFWA) according to the frequency at which the water table alternates between −25 cm and 25 cm within 430 days. The frequency of dry-wet alternating is the number of days when the water table alternates between −25 cm and 25 cm divided by the total number of observation days.

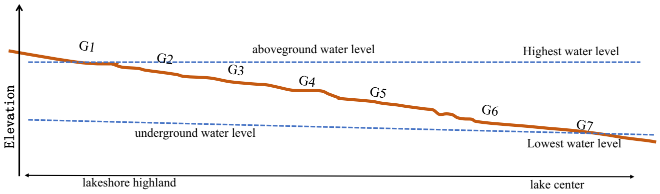

Fig. 2. Schematic diagram of relative positions of each hydrological gradient.

2.3. Plant and soil survey, sample collection and chemical analysis

The plant community and soil surveying and sampling were carried out in May 2021. The study plot just experienced the extreme dry year in 2019 and the extreme flood year in 2020. In May 2021, the research plot has been out of the water for 7 months, when the biological day peaked in the Poyang Lake wetland. In each 1-m × 1-m plot, the plant coverage, species name, species abundance and plant height were first measured and recorded. All plant species identification is based on the *Flora of China* (Wu et al., 2013). Then, all the aboveground parts of the plants were removed in a quarter (50-cm × 50-cm) of the area of each 1-m × 1-m plot and placed into a kraft paper envelope. All the aboveground material was transported to the laboratory and then oven-dried at 65 °C for 96 h to a constant weight. After oven-dried, this plant material was weighed to estimate the aboveground biomass of each species in each plot and kept for further analysis.

An undisturbed soil column with a length of 10 cm, a width of 10 cm, and a depth of 30 cm was taken with a shovel in the 50-cm × 50-cm area where the plants were cut off. After measuring the depth of the root soil layer at each site, the soil column was placed into a plastic bag. All the undisturbed soil columns were transported to the laboratory, all soil and mud were cleaned with distilled water, and all the plant roots were collected and oven-dried at 65 °C for 96 h to a constant weight. After oven-dried, this root material was weighed to estimate the belowground biomass at each plot and kept for further analysis.

In addition, 3 equidistant points were chosen on the diagonal of each 1-m × 1-m plot, and a soil drill was used to remove soil from these 3 points in layers at 10-cm intervals. The total sampled depth was 50 cm. Soils collected from the same layers were mixed and packed into the same Ziplock bag. A total of 105 soil samples were collected. After all the soil samples were transported back to the laboratory, they were dried in a freeze dryer for 48 h to a constant weight.

All aboveground and belowground dried plant and soil samples were ground into powder with a ball mill, passed through a 200-mesh sieve and stored in a polyethylene bag for testing.

The total carbon (C) and total nitrogen (N) contents of all sieved soil and plant samples were measured using an elemental analyzer (Vario Max CN Analyzer, Elementar Analysensysteme GmbH, Germany). The total phosphorus (P), sodium (Na), manganese (Mn), magnesium (Mg), kalium (K), ferrum (Fe), calcium (Ca), zinc (Zn), cadmium (Cd), cobalt (Co), chromium (Cr), cuprum (Cu), and lead (Pb) contents were measured using an inductively coupled plasma optical emission spectrometer (ICPOES) (Optima 5300 DV, Perkin-Elmer, America).

2.4. Data analysis

Plant diversity was expressed with the Patrick index (*R*), Shannon–Wiener index (H′), Simpson index (*D*), Pielou index (*E*), dominance index (λ), and Whittaker *β* index (*β*), and these indices were calculated by the following equations:

$$\mathrm{R} = \mathrm{S} \tag{1}$$

$$P_i = \frac{n_i}{N} \tag{2}$$

$$H' = -\sum_{i=1}^{s} P_i \ln\left(P_i\right) \tag{3}$$

$$\mathrm{D} = 1 - \sum_{i=1}^{S} P_i^2 \tag{4}$$

$$\mathrm{E} = \frac{\mathrm{H}'}{\ln \mathrm{S}} \tag{5}$$

$$\lambda = \sum_{i=1}^{S} P_i^2 \tag{6}$$

$$\beta = \frac{\mathrm{T}}{\mathrm{S}} - 1 \tag{7}$$

where S is the number of species (species richness) in one plot, n_i is the species abundance of species *i* in one plot, *N* is the species abundance of all species in one plot, and T is the total number of species in all of the plots.

The differences in the diversity index, biomass, C, N, P, Na, Mn, Mg, K, Fe, Ca, Zn, Cd, Co, Cr, Cu, and Pb among the plots were analyzed by one-way analysis of variance (ANOVA) combined with Dunnett's T3 post-hoc pairwise comparisons (a = 0.05).

Principal component analysis (PCA) was conducted to identify the main components by describing their variability in the studied plots. A path analysis was conducted to explore the relationship among hydrological regimes, nutrients, plant species biodiversity and dominance, plant biomass, and soil carbon across the hydrological gradients. Path models were established and separately tested based on hypothetical connections among them using structural equation modeling (SEM), an advanced multivariate statistical technique that allows hypothesized testing of complex path-relation networks (Grace et al., 2012). The goodness-of-fit of the model was determined by the χ^2 test ($P > 0.05$).

All data statistics and calculations were performed using Microsoft Office Excel 2013, ANOVA analysis was performed using IBM SPSS Statistics 25 software, mapping and PCA analysis was performed using Origin 2021 and ArcGIS Desktop 10.2, and SEM operation was performed using IBM SPSS Amos 24.

3. Results

3.1. Species diversity and dominance along different hydrological gradients

To confirm the influence of hydrological gradient on wetland plant dominance and diversity, we analyzed the change characteristics of the plant dominance index and biodiversity index along the hydrological gradient. The results showed that HFWA had the highest plant dominance, while LFWA had the lowest plant dominance. The dominance index (Fig. 3a) was higher in HFWA (approximately 0.98 and 0.93), and lower in LFWA (approximately 0.68 and 0.26). The dominance index of HFWA is 44.12% and 73.06% higher than that of LFWA. The changes in the Whittaker β index were synchronized with the changes in the dominance index. The Whittaker β index in the HFWA zones was also 60.83%–70.63% higher than that of the LFWA zones (Fig. 3b). Contrary to the results observed for the dominance index, the HFWA zones had the lowest plant biodiversity, while the LFWA zones had the highest plant diversity. Species richness was lowest in the HFWA zones (approximately 2.3 and 2.6) and highest in the LFWA zones (approximately 6 and 7). The species richness in the HFWA zones was 67.14%–71.42% lower than that in the LFWA zones (Fig. 3c). The Shannon–Wiener index was lowest in the HFWA zones (approximately 0.02 and 0.13) and highest in the LFWA zones (approximately 0.61 and 0.46). The Shannon–Wiener index values obtained for HFWA zones were 70.47% and 98.01% lower than those obtained for LFWA zones (Fig. 3d). The Simpson index and Pielou index values were also the lowest in HFWA zones and highest in LFWA zones, corresponding with the changes observed in species richness (Fig. 3e, f). In summary, on wetland beaches, HFWA-region plants have higher dominance and lower plant diversity than plants in LFWA regions.

3.2. Soil carbon and plant biomass gradient variation characteristics

Do the soil carbon content and plant biomass have the same change trends as plant dominance and diversity? To answer this question, we also analyzed soil carbon content and plant biomass changes along the established hydrological gradients. The analysis results show that the soil carbon contents of the HFWA zones (Fig. 4a) were relatively high (approximately 35.15 and 36.30 g/kg), while the soil carbon contents of LFWA zones were relatively low (approximately 24.22 and 25.86 g/kg); those of HFWA zones were 35.92%—49.88% higher than those of LFWA zones. In addition, the belowground biomass (BGB) of HFWA zones (Fig. 4b) was higher (at approximately 14,392.33 and 17,102.67 g/m^2), while the BGB of LFWA zones was lower (at approximately 4759.67 and 3640.33 g/m^2); the BGB was 202.38%—369.81% higher in HFWA zones than in LFWA zones.

Additionally, the belowground biomass plus aboveground biomass (BGB + AGB) of the HFWA zones (Fig. 4c) was relatively high (at approximately 15,118.57 and 17,701.04 g/m^2), while the BGB + AGB of the LFWA zones was relatively low (at approximately 5910.78 and 4041.11 g/m^2); the BGB + AGB of the HFWA zones was 274.12%—338.02% higher than that of the LFWA zones. Similarly, the belowground biomass divided by the aboveground biomass (BGB/AGB) was higher in the HFWA zones (Fig. 4d) (at approximately 19.83 and 28.58), while that of the LFWA zones was lower (at approximately 4.13 and 9.09); the BGB/AGB of the HFWA zones was 118.15%–519.37% higher than that of the LFWA zones, indicating that the plant biomass distributions vary greatly among different hydrological gradients. The BGB proportion is much higher than the AGB proportion in the HFWA zones. In summary, the results suggest that on wetland beaches, the HFWA zones have higher plant biomasses and higher soil carbon contents than the LFWA zones.

3.3. Nutrient element gradient characteristics

Are soil carbon content and plant biomass changes related to soil nutrient content changes? To answer this question, we also analyzed the variation characteristics of the nutrient element contents in soils along the

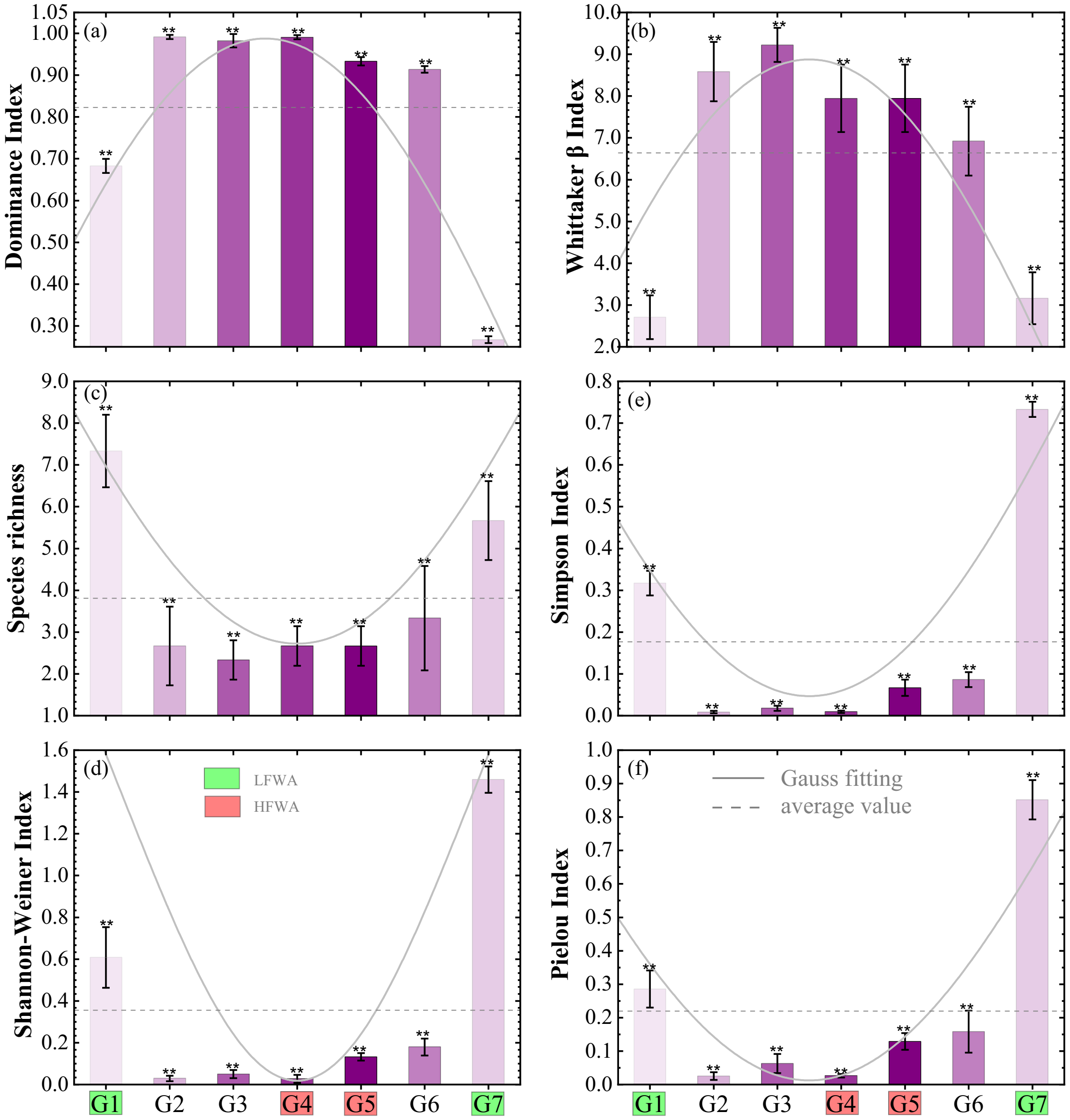

Fig. 3. Plant species diversity index values obtained for different hydrological gradients. Note: Each bar represents the mean value ± standard error; $n = 3$. For ** means significantly different among plots at the 0.01 level.

established hydrological gradients. We measured the contents of 28 elements in wetland soils. To identify the contribution of each element to the variations in the soil carbon content, we first performed PCA on the element concentrations (Fig. 5).

The results show that the first two principal components (PC1 and PC2) cumulatively explained 87% of the total variation, and the first principal component (which included P, Na, Mn, Mg, K, Fe, Ca, and Zn) explained 64.4% of the total variation, indicating that these elements are closely related to the soil carbon content ($R^2 = 0.802$, $P < 0.01$). Among the established plots, the variations in the G3, G4 and G5 gradients were most affected by the P, Na, Mn, Mg, K, Fe, Ca and Zn contents (their total combined value in the first principal component was 0.929). The results described above indicate that the P, Na, Mn, Mg, K, Fe, Ca and Zn contents have very important contributions to changes in the soil carbon content.

Are the measured changes in P, Na, Mn, Mg, K, Fe, Ca, Zn among the different hydrological gradients also consistent with the changes in soil carbon content? To answer this question, we analyzed the variation characteristics of these elemental contents along the established hydrological gradients.

The results show that the changes in the contents of these 8 elements in different gradients were synchronized with the changes in the soil carbon contents. Namely, the contents of 8 elements and soil carbon were the highest in the HFWA zones, while the contents of 8 elements and soil carbon were the lowest in the LFWA zones (Fig. 6); this result was also consistent with the changes in plant biomass (Fig. 4b, c). For example, Table 1 shows that HFWA zones had the largest P content value (approximately 0.59 g/kg), while LFWA zones had the smallest P content value (approximately 0.42 g/kg), and the maximum value was approximately 40.48% higher than the minimum value. The K content value of HFWA was the largest (approximately 17.16 g/kg), while the K content value of LFWA was the smallest (approximately 31.04 g/kg), and the maximum value was approximately 80.89% higher than the minimum value. In summary, it is shown that the change in soil carbon content is closely related to the main nutrient elements, which means that the change in soil carbon content is regulated by the main nutrient elements.

3.4. Relationship between soil carbon and influencing factors

Is plant dominance, plant biodiversity, nutrient elements, ABG and BGB, and the consistency of soil carbon content changes related to water level fluctuations of each hydrological gradients? To clarify these relationships, we statistically analyzed the distribution characteristics of the 430-day daily water level fluctuation frequency in each gradient and used the

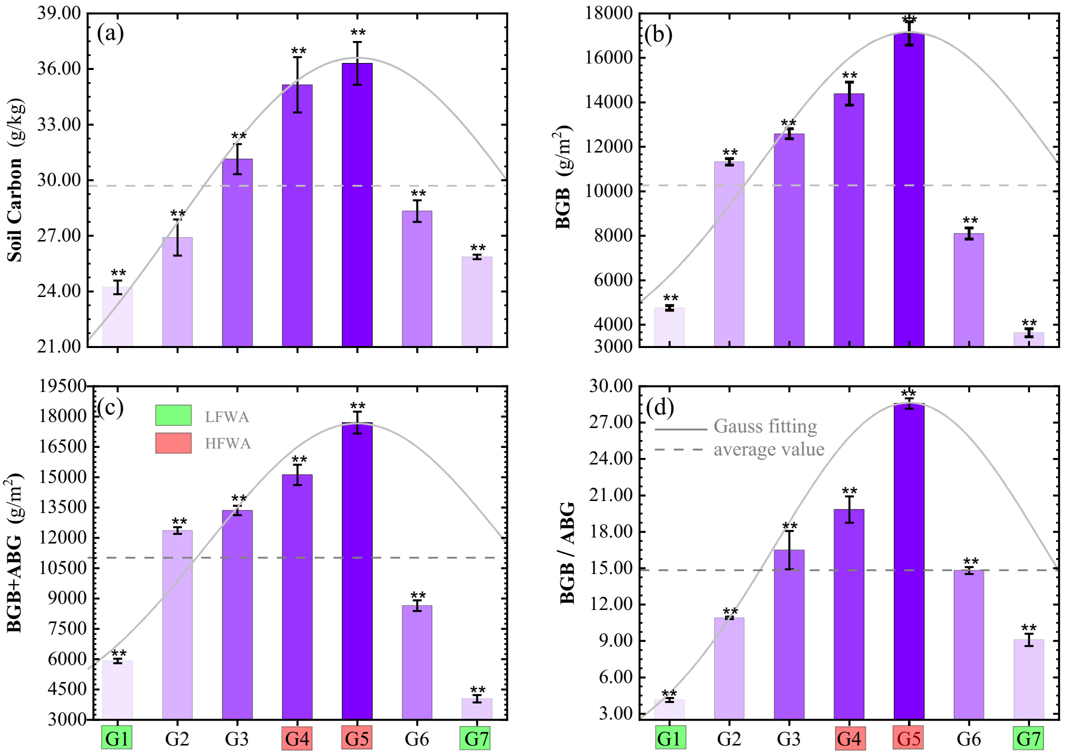

Fig. 4. Soil carbon and plant biomass measured under different hydrological gradients. Note: Each bar represents the mean value ± standard error; $n = 3$. **: significantly different among plots at the 0.01 level. BGB: Belowground biomass, AGB: Aboveground biomass, BGB + AGB: Belowground biomass plus aboveground biomass, BGB/AGB: Belowground biomass divided by aboveground biomass.

structural equation model (SEM) to comprehensively detect the relationship between them. The water level statistical analysis results show (Fig. 7) that plant dominance, plant biomass, soil carbon content, and nutrient element content of HFWA also show simultaneous changes with water level fluctuation frequency; that is, all values in HFWA are the highest, and all values in LFWA are the lowest. The LFWA (G4 and G5 gradient) has the highest frequency value (approximately 0.57 and 0.61), while the HFWA (G1 and G7 gradient) has the lowest frequency value (approximately 0.07), and the highest value is approximately 7.7 times higher than the lowest value.

Structural equation modeling (SEM) results (Fig. 8) show that the hydrological regimes are closely related to the change characteristics of soil

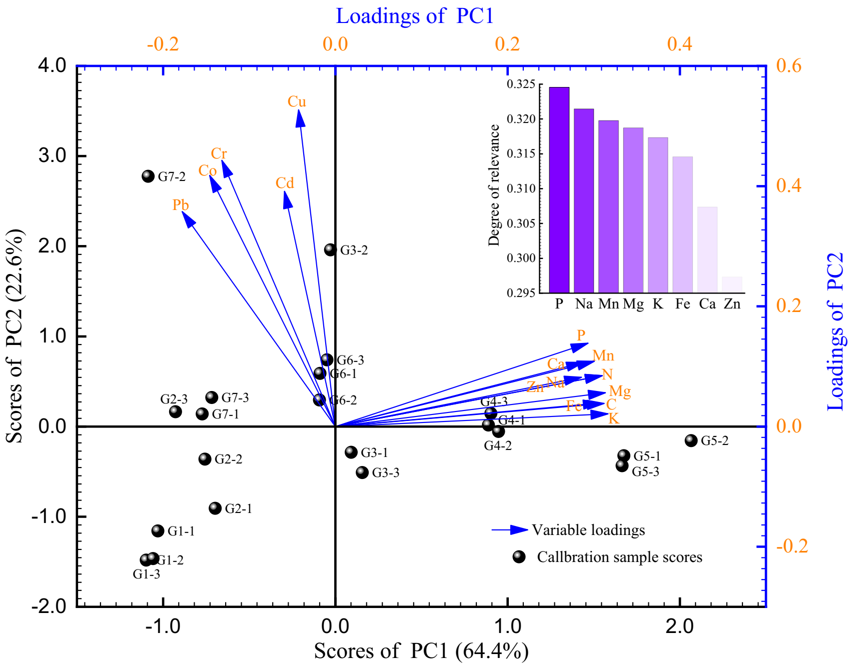

Fig. 5. PCA of nutrient element and trace element concentrations and their relationships with soil carbon. Note: G*i*-*j* represents the plot serial number, and G*i*- *j* is the *j* plot of gradient *i*.

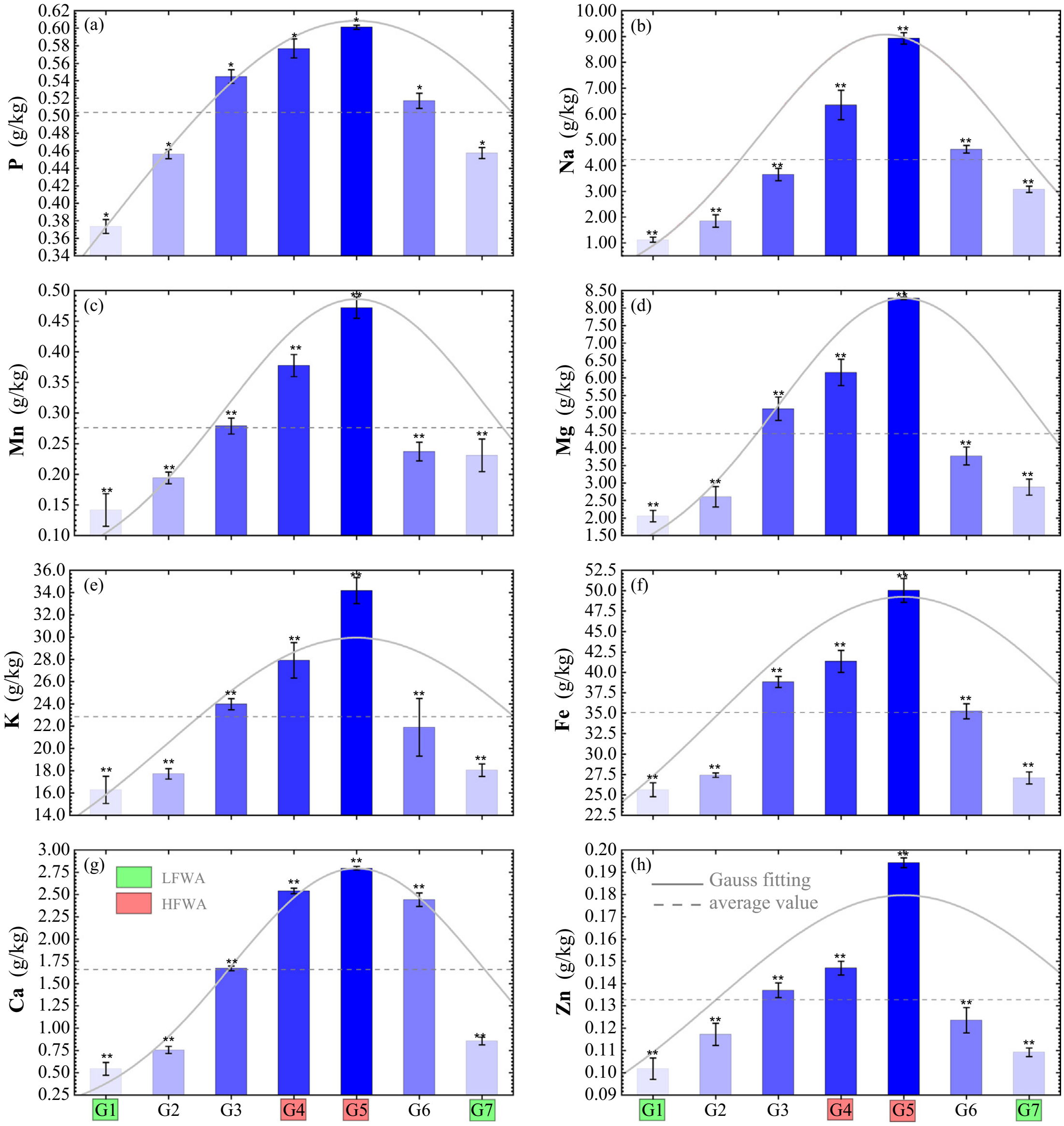

Fig. 6. Nutrient elements and trace elements under different hydrological gradients. Note: ** means significantly different among plots at the 0.01 level, * means significantly different among plots at the 0.05 level.

carbon content. The model analysis effect is very well, and the evaluation parameters are $\chi^2/df = 3.85$, RMSEA = 0.038, CFI = 0.648, IFI = 0.657, PNFI = 0.484, PCFI = 0.534. The frequency of wet-dry alternating has a very significant positive correlation with the soil nutrient element content (path coefficient = 0.88, $P < 0.001$), which shows that the high frequency of wet-dry alternating may promote a large accumulation of

Table 1
Nutrient element contents of LFWA and HFWA.

Element (g/kg)	LFWA			HFWA		
	G1	G7	Average	G4	G5	Average
P	0.37	0.46	0.42	0.58	0.60	0.59
Na	1.21	3.08	2.10	6.35	8.93	7.64
Mn	0.14	0.23	0.19	0.38	0.47	0.42
Mg	2.06	2.89	2.47	6.16	8.28	7.22
K	16.28	18.05	17.16	27.91	34.17	31.04
Fe	25.62	27.07	26.35	41.34	50.02	45.68
Ca	0.54	0.86	0.70	2.54	2.79	2.67
Zn	0.10	0.11	0.11	0.15	0.19	0.17

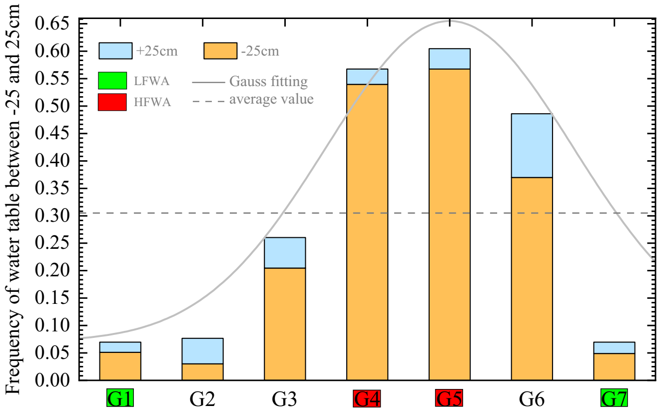

Fig. 7. Frequency diagram of the water table between-25 cm and 25 cm under different hydrological gradients.

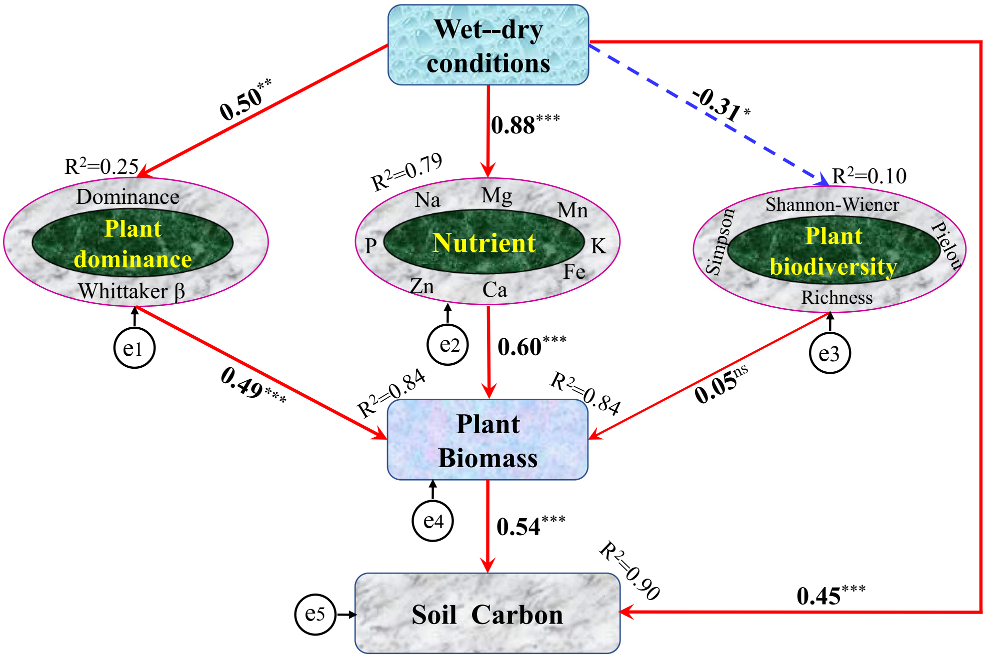

Fig. 8. Structural equation modeling (SEM) showing the relationship of hydrological regimes, nutrients, plant species diversity, and biomass on soil carbon. Note: Solid red arrows indicate positive effects and dashed blue arrows indicate negative effects. R^2 values represent total variance explained by all predictors pointing to that variable. *** means that the path coefficient is significantly different at the 0.001 level, ** means that the path coefficient is significantly different at the 0.01 level, * means that the path coefficient is significantly different at the 0.05 level, ns means that the path coefficient is not significantly different at the 0.05 level (two-tailed), and e1, e2, … means residual variable.

nutrient elements. At the same time, the nutrient element content and plant biomass also had a strong positive correlation (path coefficient = 0.60, $P < 0.001$), which indicates that higher nutrient content may promote plant productivity, thereby increasing plant biomass. On the other hand, the frequency of wet-dry alternating had a significant negative correlation with plant diversity (path coefficient = −0.31, $P < 0.05$), but it had a very significant positive correlation with plant dominance (path coefficient = 0.50, $P < 0.01$); The relationship between the changes in the two and the change in plant biomass is also very close (path coefficient = 0.49, $P < 0.001$). This shows that changes in plant diversity and dominance also had a very important impact on plant biomass. Driven by various aspects of the hydrological regimes, the ABG and BGB of dominant plants in the HFWA zones had a greater increase than that in the LFWA zone, which was also consistent with the increasing trend of soil carbon content (path coefficient = 0.54, $P < 0.001$). Last and most importantly, the frequency of wet-dry alternating also has a very significant directly positive correlation with soil carbon (path coefficient = 0.45, $P < 0.001$, Fig. 8). In summary, the hydrological regime directly affects the ABG and BGB of plants by affecting the soil nutrient content, plant biodiversity and dominance, and changes the carbon input of plants to the soil, thus having an important impact on the soil carbon content.

4. Discussion

We investigated the characteristics of plant biodiversity and plant dominance, aboveground biomass and belowground biomass, soil nutrient element content and soil carbon content along the hydrological gradient during the most prosperous period of plant growth in the Poyang Lake wetland and explored the relationship between the hydrological gradient and soil carbon content and its potential impact mechanism. The results showed that the average values of nutrient content, plant biomass and soil carbon content of HFWA were approximately 1.4 times, 2.3 times and 0.43 times higher than those of LFWA, respectively. This shows that the HFWA zones have higher soil nutrients, higher plant dominance, higher biomass and higher soil carbon content.

In addition, LFWA has low plant biodiversity and high plant dominance, and HFWA has high plant diversity but low dominance (Fig. 3). The plant dominance index changes were very consistent with the water level fluctuations, namely, the frequency of water table occurrence between −25 cm and 25 cm is higher in the HFWA and lower in the LFWA (Fig. 7). This means that water level gradient changes in wetlands had an important impact on plant diversity and species dominance (Byun et al., 2017; Gaberscik et al., 2018; Qi et al., 2021). The important reasons for this are as follows: the G1 gradient is exposed at low water levels and submerged at high water levels. It has been at the intersection of terrestrial ecosystems and wetland ecosystems for a long time. The edge effect is obvious. Mesophytes and wetland plants can coexist here. The G7 gradient is only exposed to the water surface at the lowest water level. It has been at the intersection of wetland and aquatic ecosystems for a long time, and the edge effect is also very obvious. Both wet and aquatic plants can coexist on this gradient. For the G4 and G5 gradients, the long-term water level is between −25 cm–25 cm, and the alternating frequencies between exposure and submergence are very high. Only *Carex* grass, which can tolerate drying stress and flooding stress at the same time and has very fast spread and growth rates, can survive and grow. The study of Qi et al. (2021) also showed that the plant diversity is significantly lower in high-frequency dry-wet alternating zones formed by seasonal flooding than in long-term dry zones, but community dominance is significantly higher in high-frequency dry-wet alternating zones than in the long-term dry zones and long-term flooded zones.

It is worth noting that the soil nutrient element contents are high in the HFWA zones but very low in the LFWA zones (Fig. 6). This is also very consistent with the water level fluctuations, namely, the occurrence frequency of the water table level being between −25 cm and 25 cm is higher in the HFWA zones and lower in the LFWA zones. This shows that the nutrient element contents and the wetland water regime or hydrological gradient are also very closely related; this conclusion is also confirmed by the SEM results (Fig. 8). According to our analysis, the main reasons for the accumulation of the nutrient elements in HFWA zones are as follows: (1) the G1 gradient is submerged in water for a short period of time, and the water rises and falls very rapidly along this gradient. Not only is a faster water flow speed not conducive to the hydrological, chemical or biological retention of nutrients, but it also removes the original nutrient matter. Although the G7 gradient is submerged by water for a long time, because it is connected to the lake center of the water body and the water level is constantly rising and scouring, nutrients are easily transferred to the water body along with the water, and it is difficult for nutrients to stay in the wetland soil. In the HFWA zones, the water level remains between −25 cm and 25 cm most of the time, the water flow and migration are slow, the residence time is long, and the nutrients in the flowing water and soil have sufficient opportunities to undergo physical, chemical and biological reactions and retention (Johnston, 1991; Marcé et al., 2018). (2) The G1 gradient is exposed for a long time, and the soil moisture conditions are insufficient in this gradient. The G7 gradient is in a flooded state for a long time and is often in an anaerobic environment. Neither of these conditions is conducive to the mineralization of microorganisms or the production of nutrient-retention conditions. However, the HFWA zones are often in states of alternating dry and wet conditions with high alternating frequencies. The groundwater level and flooding are not very deep, the water and oxygen levels are relatively sufficient, and nutrient migration is slow. This situation is conducive to the mineralization of organic matter by microorganisms and the production of nutrient-retention conditions (Noe et al., 2012). (3) Although the plant species diversity was high in the LFWA zones, the dominant species were not obvious, the growth of each species was not good, and the biomass was relatively low. Therefore, the plants returned fewer nutrients to the soil. In contrast, the dominant species of the HFWA zones were particularly obvious, productivity and biomass were very high, and plants returned more nutrients to the soil (Huang et al., 2015). Driven by hydrological processes, the soil nutrient contents were low in the LFWA zones, while the soil nutrient contents of the HFWA zones were relatively high. Although many plants do not grow well in barren environments, they have the opportunity to compete for survival (Ceulemans et al., 2013); however, in fertile soils, competitive plants are not limited by nutrients or water, their dispersal and growth speeds are extremely fast, and their root systems are plaguily dense(Hautier et al., 2009; Stevens et al., 2010). Under these conditions, the belowground biomass can be very large and can quickly spread and occupy the living space, forming dominant species. Other less competitive species have difficulties spreading and surviving. Therefore, nutrients are another important reason why LFWA zones have low plant biodiversity and high plant dominance.

This study found that the soil carbon content was lower in zones with high biodiversity but high in zones with low plant diversity in wetland ecosystems; this result differs from the results of studies conducted in arid and semiarid grassland ecosystems. In grassland ecosystems, soil carbon contents are generally higher in zones with high biodiversity, and it is believed that biodiversity increases the soil carbon content in these ecosystems. This is mainly because grassland ecosystems are stimulated by increased biodiversity, greatly improving plant productivity and, in turn, increasing the amount of carbon that is input to soils (Fornara and Tilman, 2008; Steinbeiss et al., 2008; Cong et al., 2014; Yang et al., 2019). The reason for this inconsistency between wetland and grassland ecosystems is their different environmental conditions. Grassland ecosystems are generally not strongly disturbed by hydrological processes but are often limited by nutrient conditions. When biodiversity increases, species with strong carbon or nitrogen fixation capabilities, such as C4 plants and legumes, appear. The presence of these species improves the nutrient conditions of the soil and increases the productivity of the entire plant community, thereby increasing the return of carbon and nitrogen to the soil by plants (Fornara et al., 2013; Jackson et al., 2017). Conversely, the increased soil carbon and nitrogen contents have a positive feedback on plant productivity by enhancing the mineralization of nitrogen and other nutrient elements, further accelerating the long-term storage of soil carbon (Cong et al., 2014).

Based on the research results described above, we can infer that the changes in the hydrological process of the wetlands around Poyang Lake have led to the accumulation of soil nutrient elements in HFWA zones, reduced plant biodiversity, and increased the dominance of dominant plants, thus increasing the productivity of dominant plants, especially the belowground parts of these plants. Increased productivity increases the ability and total amount of carbon input into the soil by plants, which in turn increases the carbon content of the soil.

In the context of increasing global temperatures and a continuous increase in the concentration of carbon dioxide in the atmosphere, a series of changes are expected to occur in global precipitation patterns, ecosystem productivity and species distribution patterns. If global rainfall continues to increase, the high-water level of the Poyang Lake wetland region will be extended, the depth of flooding will increase, and the dominant species will inevitably change. The current water level in the range of −25 cm and 25 cm may shift toward the lakeshore highlands, and the area may also experience changes or disappear. The plant biodiversity and dominant species in the region may also change. This series of changes will cascade and affect the carbon sequestration and carbon storage capacities of wetlands. Therefore, we need to use longer monitoring hydrological, plant community, soil nutrient, organic decomposition, nitrogen mineralization, and microorganism data sequences to further clearly explore the external and internal mechanisms affecting the carbon fixation and carbon storage capacities of wetlands. Effective measures should be taken in advance to better address this series of problems introduced by future global changes.

5. Conclusion

Wetland ecosystems play a very important role in global carbon storage. To better understand this importance, we investigated the characteristics of plant biodiversity and plant dominance, aboveground biomass and belowground biomass, soil nutrient element contents and soil carbon contents along hydrological gradients in the Poyang Lake wetlands and explored the relationship between these hydrological gradients and soil carbon contents as well as the potential corresponding impact mechanism. We found that water level changed high frequency among −25 cm and 25 cm may led to the accumulation of soil nutrient elements, reduced plant biodiversity, but increased the productivity of dominant plants, especially the belowground parts of these plants. The increased productivity could increase the ability and total amount of carbon input into the soil by plants, which in turn increases the carbon content of the soil. These results profoundly revealed the mechanism by which wetland hydrological gradients regulate the concentrations of nutrient elements and thereby affect vegetation growth and carbon sequestration, and provide a new cognitive basis for understanding the coupling of carbon and water. Our findings have strong implication for the verification of global wetland carbon sources/sinks, which can provide a certain scientific basis for achieving global carbon neutrality and carbon peaking goals.

CRediT authorship contribution statement

Quanjun Zhang implemented laboratory analysis of samples, curated the data, conceptualized and wrote the original manuscript. Zhaosheng Wang conceptualized and revised the manuscript. Xiubo Yu, Quanjun Zhang and Shaoxia Xia discussed and designed the experiments. Xiubo Yu, Shaoxia Xia, Quanjun Zhang, Suxiao Li and Dingkun Yu participated in and conducted the field survey and sampling together. Zhaosheng Wang and Guangshuai Zhang reviewed and edited the manuscript. Xiubo Yu reviewed the manuscript and raised funds to support this study.

Declaration of competing interest

The authors declare that there are no conflicts of interest.

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