

Comparison on soil organic carbon within two typical wetland areas along the vegetation gradient of Poyang Lake, China

Xiaolong Wang, Ligang Xu and Rongrong Wan

ABSTRACT

Poyang Lake is an important wetland with international significance in biodiversity conservation and local carbon cycle. A study was conducted to investigate the effects of vegetation communities on seasonal and spatial variations of soil organic carbon (SOC) and dissolved organic carbon (DOC) in two dominant wetlands (dish-shaped pit wetland and delta wetland) of Poyang Lake, China. Results revealed significant variations of SOC and DOC along the vegetation gradient. Maximum accumulation of SOC and DOC was produced in *Phragmites* community, and the minimum ones in *Phalaris* community both in spring and in autumn. In comparison with delta wetland, dish-shaped pit wetland obtained higher SOC within the same vegetation type, which indicated that soils of dish-shaped pit wetland had greater capacity to store carbon. Compared with SOC, DOC represented stronger seasonal variations with great increase in autumn, which suggested that DOC was more sensitive to hydrology processing. Furthermore, significant variations of SOC and DOC were closely related to vegetation biomass both in spring and in autumn. Moreover, elevation and gradient also affected the distributing pattern of organic carbon suggesting significant influence of topography characteristics on the carbon pool.

Key words | Poyang Lake, seasonal variation, soil organic carbon, vegetation community

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INTRODUCTION

Wetlands are usually characterized by large biomass, low temperature, high humidity, and weak microbial activity (Tockner & Stanford 2002). Covering a small proportion of the Earth's land surface, wetlands contain a large proportion of the world's carbon (approximately between 18% and 30%, depending on definition) stored in terrestrial soil reservoirs and represent 15% of the terrestrial organic matter loss to the oceans (Stern *et al.* 2007). Hence, wetlands represent one of the largest biological carbon pools and play a decisive

role in the global carbon cycle (Mitsch & Gosselink 2000). Research in this area is needed to quantify more accurately the extent of wetlands' soil carbon pool worldwide, the importance of wetland type, hydrological fluctuations, and plant biomass of these pools (Biol *et al.* 2010).

Many studies have reported on the variations of soil organic matter and related influences on wetland systems at various scales (Friborg & Soegaard 2003; Blanca & William 2008; Liu *et al.* 2015). Accumulation of organic matter in wetland soils depends on the ratio between inputs (organic matter produced *in situ* and *ex situ*) and outputs (decomposition and erosion) of organic matter, which is strongly related to many factors including climate, wetland type, hydrology regime, soil properties, primary production, and

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microbial activities (Anderson *et al.* 2009; Bills *et al.* 2010; Boyd *et al.* 2010; Wang *et al.* 2014a, 2014c). Climate is sometimes an important factor determining the soil carbon pool in wetland systems because temperature controls the decomposition rate of soil organic carbon (SOC) (Malmer *et al.* 2005; Lloyd 2006; Gudas *et al.* 2010; Dong *et al.* 2012). However, anaerobic conditions and high productivity of the vegetation community are two key factors which enhance carbon accumulation in wetland soils (Li *et al.* 2008; Dai *et al.* 2014). The hydrologic regime has been considered as the driving force in wetland systems, which directly changes the wetland physicochemical properties, especially oxygen availability that controls the ratio of organic matter decomposition (Zweifel 1999; Tranvik *et al.* 2009; Chen *et al.* 2011; Oana *et al.* 2014). Carbon pools are generally greater in permanently flooded sites than those in pulsing hydrologic sites, because alternation of wetting and drying substantially enhances the oxidation of organic matter, especially of soil dissolved organic carbon (DOC) which is an energy source for soil and aquatic organisms and is involved in the transport of nutrients, pollutants, and metal ions in wetland systems (Machate *et al.* 1997; Juutinen *et al.* 2001).

On the other hand, vegetation is an important biological factor in the ecological succession of wetlands, and the main factor affecting the carbon storage and carbon fixation in wetland ecosystems (Joabsson & Christensen 2001; Mei & Zhang 2007). Furthermore, vegetation is more important sometimes than microclimate, soil, slope, and elevation in controlling the variation of SOC and DOC in some wetland systems (Malmer *et al.* 2005; Li *et al.* 2008). Plant litter is one of the most abundant carbon sinks in wetlands (Lloyd 2006; Wang *et al.* 2013). Most labile organic compounds in wetland soil, such as sugars, amino acids, and volatile fatty acids are leached out either from the senescent or dead plant biomass by abiotic and biotic effects (Li *et al.* 2008; Xu *et al.* 2013). Changes in the dominant species within the plant community may alter ecosystem structure and material cycling processes, which, in turn, change soil carbon pools through changes in the quantity and quality of organic material input into wetland soils (Mei & Zhang 2007; Gan *et al.* 2009). Furthermore, diversity of micro-topography in natural wetland systems also plays a key role in affecting spatial distribution of soil organic matter (Steenwertha *et al.* 2008). The relationship between wetland productivity (vegetation, soils, water)

and soil organic matters is complex (Moore *et al.* 2002). The intricate dynamics of SOC and DOC as well as the related factors in wetland systems are not yet well understood.

Poyang Lake is the largest freshwater lake in China and its wetland ecosystems are globally significant in terms of biodiversity and carbon cycling (Zhu 1997; Dong *et al.* 2012). In recent years, the water level of Poyang Lake has exhibited unusual fluctuation, including frequent drought events in the lake, which in return affects natively the lake ecosystem (Zhang *et al.* 2012b; You *et al.* 2015; Zhang & Werner 2015). Interest in wetland ecosystem processes of the lake have been greatly increased during the past decade (Wu *et al.* 2009; Dong *et al.* 2012). Research, to date, on the lake has primarily focused on the hydrology process, water quality, vegetation ecology, and pollution distribution, as well as their relations with hydrological conditions of the lake (Hu *et al.* 2011; Jin *et al.* 2011; Zhang *et al.* 2012b; Wang *et al.* 2012, 2014a; Xu *et al.* 2015). Moreover, variation of active carbon in surface soil has been demonstrated in relation to vegetation succession and wetland types (Zhang *et al.* 2012a; Wang *et al.* 2016). Previous studies have well illustrated the hydrological regime and its dominant role in the wetland system functions, such as variation of water quality and plant distribution (Jin *et al.* 2011; You *et al.* 2015; Tan *et al.* 2015). However, spatial patterns of soil organic matter accumulation in different wetland types, especially along vegetation gradients under different micro-topography, in Poyang Lake are not well known. It is crucial to understand the significance in the global carbon cycle of those wetlands that are characterized with high amplitude water level fluctuation in middle-to-lower reaches of the Yangtze River (Dong *et al.* 2012). The main objectives of this paper were to distinguish the spatio-temporal variations of soil organic matter in two dominant types of wetlands (dish-shaped pit wetland and delta wetland) with different micro-topography and hydrologic process, and to identify the relations of SOC and DOC to vegetation distribution.

STUDIED AREAS AND METHODS

Study area

Poyang Lake is situated in the northern part of Jiangxi Province with a humid subtropical climate as it is strongly

influenced by the East Asian monsoon. Characterized by diverse topography and complex hydrologic regime, the lake is a compound multi-type wetlands system consisting of lakes, deltas, rivers, flood plains, marsh, and so on (Zhu 1997; Dai *et al.* 2015). Furthermore, Poyang Lake has exhibited great seasonal fluctuation in water level with more than 10 m difference between the lowest and the highest mean monthly water level, which exposes vast grass-covered marshland during the dry season from November to April of the coming year (Wang 2005). Poyang Lake delivers various ecosystem services, such as water resource supply, flood-water storage, biodiversity maintenance, and pollution retention. The lake is particularly important to the conservation of the endangered Siberian crane, more than 95% of whose world population congregates here during the winter (Wu & Jin 2002).

Due to the interaction of landform and river systems, the landscape pattern of Poyang Lake is dominated by dish-

shaped pit wetland and delta wetland, which support the ecological function of the lake such as biodiversity maintenance and biogeochemical cycles. In this study, Bang Lake (BL) and Ganjiang main-branch delta (GD) wetlands, located in the northern part of Poyang Lake, were selected as study areas as typical cases of dish-shaped pit wetland and delta wetland, respectively (Figure 1). Located to the north of Wu town, BL is an important migratory bird habitat with a total water area of 95 km² in the monsoon season and about 26 km² in the dry season. The unique water regime forms an orbicular vegetation zone in BL, with *Potamogeton malaianus* and *Hydrilla verticillata* communities, *Phalaris arundinacea* community, *Carex cinerascens* community, and *Phragmites communis* and *Triarrhena lutarioriparia* communities distributed from the bottom up along the altitudinal gradient. GD is located in the east of BL, and is a typical alluvial delta of the Ganjiang River with a total area of 37 km². Inundation and exposure of the Ganjiang

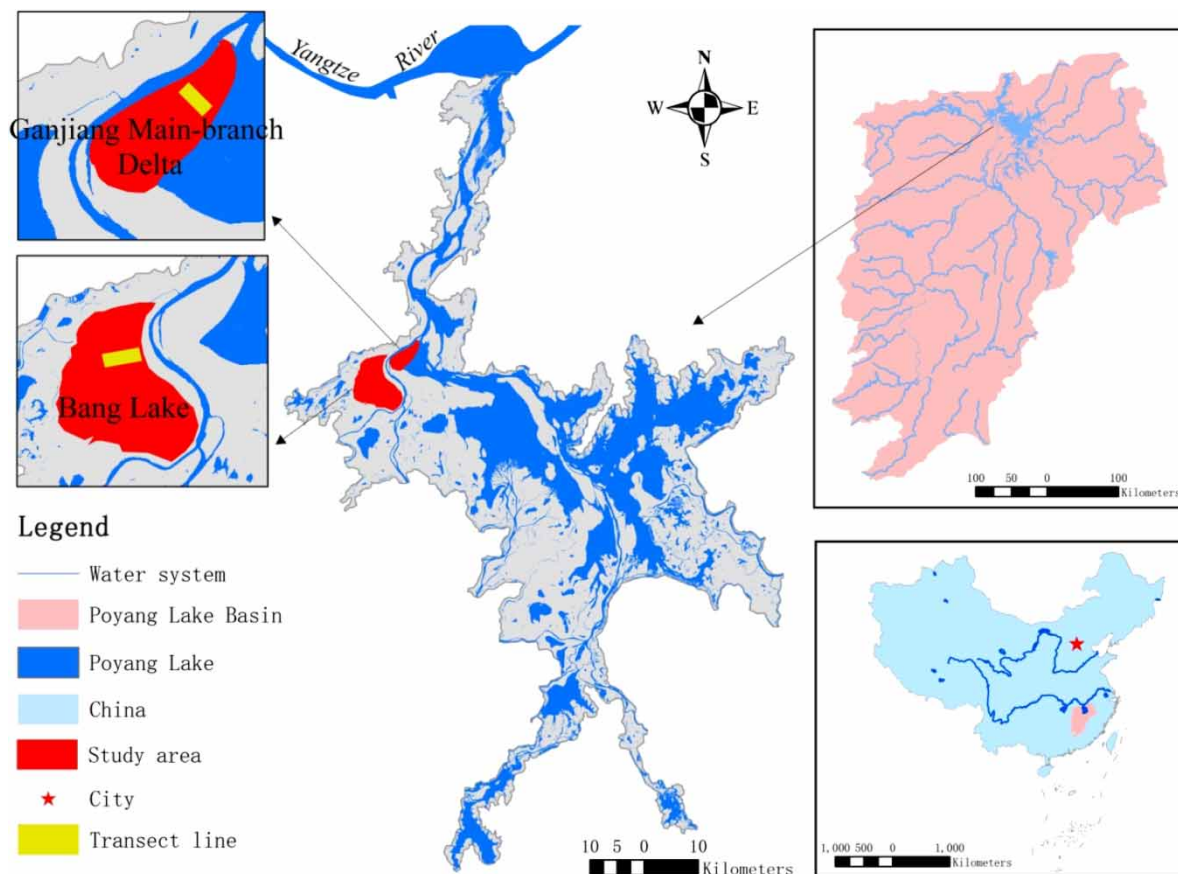


Figure 1 | Locations of the two studied typical wetlands in Poyang Lake.

main-branch delta are controlled by water level fluctuation in the main body of Poyang Lake characterized by relatively rapid flooding and receding (Li & Zhang 2015). Vegetation distributing patterns of GD are successively *Phalaris arundinacea* community, *Carex cinerascens* community, *Aremisia selengensis* community, and *Phragmites communiss* and *Triarrhena lutarioriparia* community from the bottom up. The soil type of the two wetlands is meadow soil and texture is sandy loam soil (Wang 2005).

Sampling site and surveying

There are two growing seasons for the dominant plants in a single year, before and after flooding, respectively, in Poyang Lake (Wang et al. 2014a, 2014b). Accordingly, the contents of soil carbon of three accordant zonal vegetation communities, viz., *Phalaris* community, *Carex* community, and *Phragmites*, in BL and GD were studied in April and November 2013, respectively, to avoid the flooding season. One transect line was placed along the altitudinal gradient in both BL and GD, respectively. Three quadrates were randomly established as duplicates through throwing pine frames (1 m × 1 m) along the transect line within

each zonal vegetation community (Mitsch & Gosselink 2000).

About 500 g multipoint mixed undisturbed soil was sampled from a 0 to 10 cm layer by stainless steel drilling at each quadrate and then preserved in a polyethylene sealed bag. All the soil samples were stored at 4 °C and transported to laboratories within 24 h. At the same time, the geographic coordinates of each plot were recorded by GPS (GPS 60, GARMIN). Gradient was determined by a multi-functional slope measuring instrument (JZC-B2.050). Vegetation community coverage was estimated using the nine-grade Braun-Blanquet scale (Van der Welle & Vermeulen 2003). Detailed information of each species per quadrate, including height, amount, and phenological phase, were recorded on the spot. All plants in the quadrate were excavated carefully using a stainless steel spade (WJQ-308) to 30 cm depth for *Phalaris arundinacea* community and *Carex cinerascens* community, and 40 cm depth for *Phragmites communiss* community to ensure all roots were collected. Above-ground and below-ground parts of all plants were snipped after removing soil particles on the stubbles and roots, and then weighed by electronic platform scale in the field. The general conditions of each vegetation community are included in Table 1.

Table 1 | Descriptions of plots for three vegetation communities of two typical wetlands in Poyang Lake

Wetlands	Vegetation community	Code	Elevation (m)	Gradient (%)	Soil type	Constructive species	Companion species
BL (dish-shaped pit wetland)	<i>Phragmites communiss</i>	<i>Phragmites-B</i>	16–18	3–5	Loam soil	<i>Phragmites communis</i> <i>Trin</i>	<i>Triarrhena lutarioriparia</i> L, <i>Carex cinerascens</i> Kukenth, <i>Aremisia selengensis</i> Turcz,
	<i>Carex cinerascens</i>	<i>Carex-B</i>	14–16	0–2	Loam/clay soil	<i>Carex cinerascens</i> Kukenth	<i>Sagittaria sagittifolia</i> , <i>Cardamine lyrata</i> , <i>Herba Gnaphaii Affinis</i>
	<i>Phalaris arundinacea</i>	<i>Phalaris-B</i>	13–14	0–5	Loam soil	<i>Phalaris arundinacea</i>	<i>Polygonum hydropiper</i> L, <i>Echinochloa crusgalli</i>
Ganjiang main-branch delta (river alluvial delta)	<i>Phragmites communiss</i>	<i>Phragmites-G</i>	17–18	4–15	Sandy/loam soil	<i>Phragmites communis</i> <i>Trin</i>	<i>Triarrhena lutarioriparia</i> L, <i>Carex neurocarpa</i> Maxim, <i>Cynodon dactylon</i> , <i>Aremisia selengensis</i> Turcz, <i>Potentillalimprichtii</i> J. Krause
	<i>Carex cinerascens</i>	<i>Carex-G</i>	15–16	3–12	Loam soil	<i>Carex cinerascens</i> Kukenth	<i>Gnaphaii Affinis</i> , <i>Aremisia selengensis</i> Turcz, <i>Conyza canadensis</i>
	<i>Phalaris arundinacea</i>	<i>Phalaris-G</i>	14–15	5–18	Sandy/loam soil	<i>Phalaris arundinacea</i>	<i>Lobeliae Chinensis</i> , <i>Alopecurus aequalis</i> Sobol, <i>Rumex japonicus</i> , <i>Polygonum plebeium</i>

Sample and data analysis

Soil samples were homogenized in a grinder after removal of any visible live plant material, after which they were passed through a 2-mm sieve to remove rock fragments and large organic debris. Soil moisture was determined by first drying fresh subsamples from each soil sample at 105 °C for 24 h, and then calculating the difference in weights between fresh sample and oven-dried sample. Soil type was determined according to the ratio of sand and clay particles using a hydrometer method (Tan 1996). The percentage of soil organic matter content was measured by loss on ignition at 500 °C for 4 h (Bruland & Richardson 2004). SOC was calculated by weight difference between ash and sample. Fresh soil samples (equivalent to 10 g oven-dried weight) were extracted with 30 mL distilled water for 30 min on an end-over-end shaker at approximately 240 rpm and centrifuged for 20 min at 8,000 rpm (Ghani *et al.* 2003). All supernatants were filtered through a 0.45-µm filter into separate vials for DOC analysis (total organic C-VCPH C analyzer, Shimadzu, Kyoto, Japan). Total nitrogen was measured using a Carlo Erba CNS analyzer (Milan, Italy). Total phosphorus (TP) was determined by the TP ashing method and analyzed by the ascorbic acid colorimetric procedure (Technicon Autoanalyzer II, Terrytown, NY, USA). Available nitrogen was determined using a 10-day anaerobic incubation, followed by extraction with 0.5 M K₂SO₄ (Lu 1999). Extracts were analyzed for NH₄⁺-N using an automated colorimetric analysis (EPA365.1 Technicon Autoanalyzer). Available phosphorus was also determined using a 10-day anaerobic incubation and analyzed by the ascorbic acid colorimetric procedure (Lu 1999).

After data entry, importance value (IVc) of species for each plot was calculated by Equation (1) to value the dominance of species:

$$IVc = \frac{RDc + RCc + RFc}{3} \quad (1)$$

among which IVc, RDc, RCc, and RFc refer to the importance value index, relative density, relative coverage, and relative frequency of the constructive species, respectively. The Shannon–Wiener index was calculated to estimate the

species diversity of communities:

$$H_j = - \sum_{i=1}^s p_i \ln p_i \quad (2)$$

where H_j is Shannon–Wiener index, representing species diversity of the j th plot; p_i refers to the rate of the i th species amount to the sum amount of entire community in the j th plot; S is the number of plant species in the community. The Margalef index was calculated to estimate the species richness of each vegetation community:

$$R = \frac{S - 1}{\ln P} \quad (3)$$

where R refers to the species richness value, S is the number of plant species in the community, and P is the total number of plants within each quadrat (Tan 2009).

Average data, range, and standard deviation (SD) of physicochemical characteristics of surface soil and characteristics of vegetation communities were determined based on pooled samples (three reduplicate samples at each plant community). Non-normality of the data was treated by taking a logarithm or square root, whenever appropriate after normality assessment by Kolmogorov–Smirnov test (Tan 2009). Differences between means were tested by Turkey's means comparison test for post hoc multiple comparisons. Principal component analysis (PCA) was employed to sort the variables of soil microbial biomass, soil physicochemical conditions, and vegetation community characteristics based on seasonal datasets. Factor loading was defined to explore the nature of variation and principal patterns among them using varimax for factor rotation. Any factor with an eigenvalue greater than unity (eigenvalue > 1) was selected as significant. All statistic analyses, including One-way analysis of variance (ANOVA) and two-tailed test, were conducted using SPSS 13.0 statistical software package, and significance was determined at the 95% confidence level.

RESULTS

Daily fluctuation of water level of BL and GD

Figure 2 shows the water level fluctuations of BL and GD in 2013. The water level of Poyang Lake generally increases

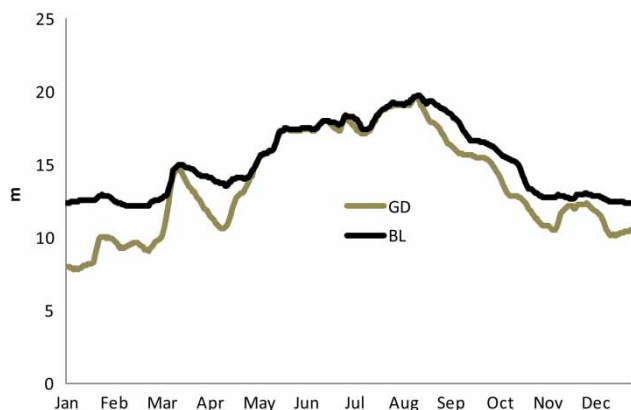


Figure 2 | Daily fluctuation of water level in GD and BL in 2013.

from March due to plum rain, and reaches a peak in August because of the blocking effects of the Yangtze River, and then continuously decreases until the rainy season of the next year (Zhu 1997). The water level fluctuation of GD is directly controlled by that of the main body of Poyang Lake. Accordingly, similar daily water level fluctuation was found for GD in 2013. Less difference was found in the daily water level between GD and BL in the flooding season (from April to September). However, BL maintained a significantly higher water level than that of GD in the dry season in 2013. Furthermore, the water level of BL rapidly rises with that of Poyang Lake as the wet season progresses; however, it slowly decreases during the dry season due to its semi-enclosed micro-topography (Wang 2005; Zhang & Werner 2015).

SOC and DOC contents

Results of SOC analysis are summarized in Table 2. The highest SOC (42.29 g/kg) was found in the *Phragmites*

community of BL (*Phragmites-B*), followed by *Phragmites* community of GD (*Phragmites-G*), *Carex* community of BL (*Carex-B*), and *Carex* community of GD (*Carex-G*), while the lowest organic carbon (11.79 g/kg) was observed in the *Phalaris* community of GD (*Phalaris-G*) in spring. Under the same vegetation community, the *Phalaris* community of BL (*Phalaris-B*) produced higher SOC than *Phalaris-G* in spring. Less seasonal variance was found in SOC contents among the studied vegetation communities.

Significant seasonal variations of DOC were found in typical wetlands of Poyang Lake. Obviously, DOC content of each vegetation community in autumn was higher than that in spring. However, *Carex-B* demonstrated the highest DOC contents both in spring and autumn. Similar to SOC, DOC of *Phalaris-B* was higher than that of *Phalaris-G*, with the latter determined to have the lowest contents of DOC. Accordingly, *Carex-B* showed the highest ratio of DOC/SOC with the values of 1.26% (in spring) and 1.81% (in autumn). However, relatively low ratios of DOC/SOC were found in *Phragmites-B*. Averaging across the vegetation zone, ratios of DOC/SOC in two typical wetlands were higher in autumn than those in spring.

Typical vegetation community's characteristics

Coverage values of studied vegetation communities in spring, varying from 80% to 100%, were higher than those in autumn (65%–95%) (Table 3). *Carex-B* had the highest seasonal coverage values, while *Phalaris-G* showed the lowest values in spring. Moreover, *Phragmites-G* had the highest average species height, while *Carex-G* and *Carex-B* were found to have the lowest constructive species height

Table 2 | Seasonal variations of SOC and DOC of three vegetation communities in two studied typical wetlands in Poyang lake

Vegetation community	SOC (g/kg)		DOC (mg/kg)		DOC/SOC (%)	
	Spring	Autumn	Spring	Autumn	Spring	Autumn
<i>Phragmites-B</i>	42.29a* ± 7.41	43.62a ± 7.59	353.56b ± 57.36	454.03b ± 113.01	0.84 ± 0.30	1.04 ± 0.43
<i>Carex-B</i>	33.77b ± 6.36	35.53ab ± 7.07	426.97a ± 33.26	655.57a ± 86.13	1.26 ± 0.34	1.81 ± 0.51
<i>Phalaris-B</i>	22.28c ± 2.99	22.57c ± 2.15	191.61c ± 53.13	256.01c ± 70.69	0.86 ± 0.32	1.13 ± 0.37
<i>Phragmites-G</i>	36.73ab ± 14.13	36.64ab ± 9.08	318.93b ± 51.75	417.12b ± 99.67	0.87 ± 0.38	1.14 ± 0.47
<i>Carex-G</i>	29.21b ± 4.47	30.57b ± 4.61	284.22b ± 65.79	334.73bc ± 98.73	0.97 ± 0.25	1.07 ± 0.48
<i>Phalaris-G</i>	11.79d ± 3.55	10.33c ± 2.02	111.65d ± 18.64	130.05d ± 12.87	0.95 ± 0.21	1.03 ± 0.29

* Different letters in the columns indicate significant differences for $P \leq 0.05$.

Table 3 | Descriptions typical vegetation communities in Poyang Lake

Vegetation community	Vegetation community coverage (%)		Constructive species height (cm)		Constructive species importance value	
	Spring	Autumn	Spring	Autumn	Spring	Autumn
<i>Phragmites-B</i>	85ab* ± 10	85ab ± 5	115.2b ± 35.1	188.3a ± 48.3	56.5d ± 9.6	66.8b ± 13.5
<i>Carex-B</i>	100a ± 5	95a ± 5	65.6d ± 15.6	68.7b ± 13.2	93.3a ± 3.5	90.2a ± 2.9
<i>Phalaris-B</i>	85ab ± 10	65c ± 10	78.8c ± 7.8	35.2c ± 11.5	90.7a ± 4.1	57.9bc ± 6.0
<i>Phragmites-G</i>	95a ± 5	85ab ± 5	202.5a ± 44.5	225.1a ± 35.2	75.8c ± 11.3	64.1b ± 11.5
<i>Carex-G</i>	95ab ± 5	90a ± 5	51.7d ± 3.5	46.5b ± 2.3	91.5a ± 6.5	88.3a ± 7.2
<i>Phalaris-G</i>	80b ± 10	70c ± 10	79.6c ± 4.6	32.2c ± 2.71	83.2b ± 7.3	52.7c ± 9.5

* Different letters in the columns indicate significant differences for $P \leq 0.05$.

in spring. However, *Phalaris-G* and *Phalaris-B* showed the lowest constructive species height in spring with values of 32.2 cm and 35.2 cm, respectively.

Less variation of constructive species importance value between spring and autumn was found in *Phragmites-B* and *Phragmites-G* (Table 3). Constructive species were absolutely predominant in the *Carex* community. Furthermore, *Phalaris-B* and *Phalaris-G* also showed relatively high predominance of constructive species in spring. However,

the constructive species importance values of the *Phalaris* community decreased remarkably in autumn.

Seasonal variations in above-ground and below-ground biomass of the studied vegetation communities were observed (Figure 3(a) and 3(b)). *Phragmites-G* produced the highest seasonal above-ground biomasses. Less difference of above-ground biomasses was found between *Carex-B* and *Carex-G*. However, *Phalaris-G* and *Phalaris-B* had the lowest above-ground biomass with great decreases in

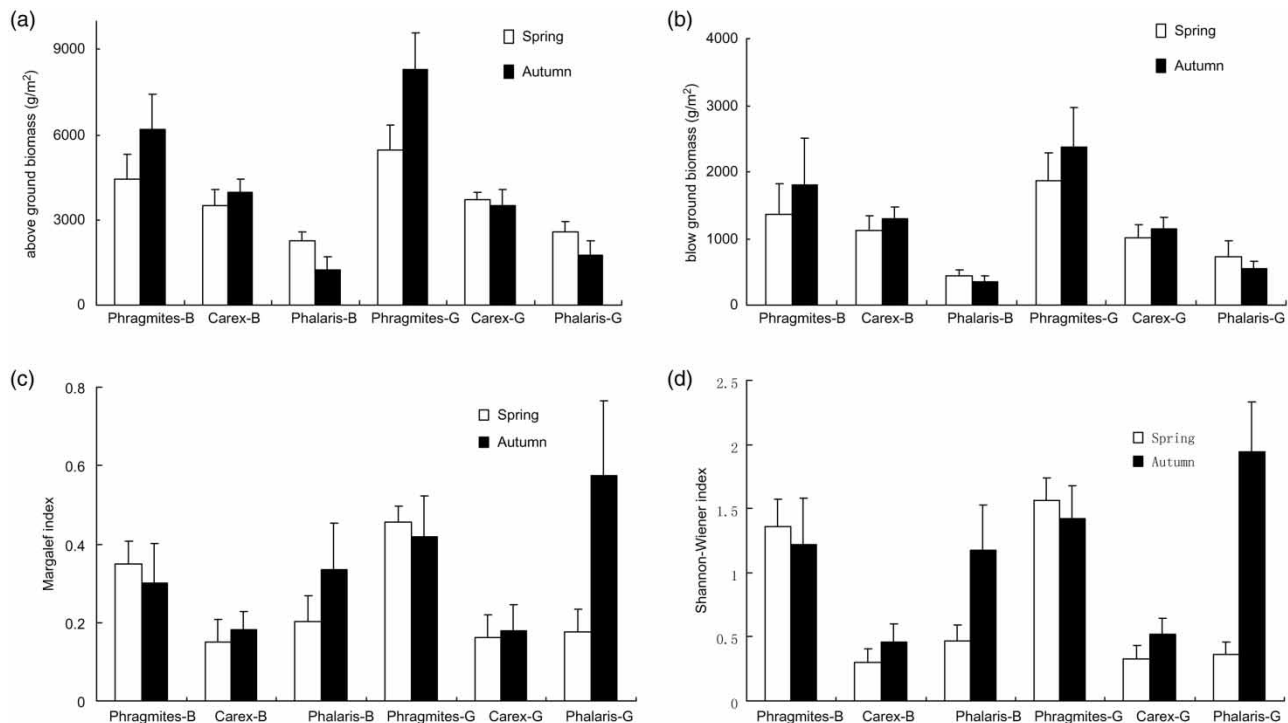


Figure 3 | Seasonal average values and SD of above-ground biomass (a), below-ground biomass (b), Margalef index (c), and Shannon-Wiener index (d) of vegetation communities in two typical wetlands.

autumn, which were in contrast to that of *Phragmites-B* and *Phragmites-G*. Compared with above-ground biomass, relatively lower below-ground biomass was determined in vegetation communities of the two wetlands with values in the ranges of 428.7 g/m²–1,866.0 g/m² in spring and 342.7 g/m²–2,363.4 g/m² in autumn, respectively.

Phragmites-G represented the highest species richness in spring, while *Phalaris-G* showed the highest one in autumn (Figure 3(c)). *Carex-B* and *Carex-G* demonstrated less seasonal variation of species richness with relatively low Margalef indexes. In contrast to the Margalef index, the highest Shannon–Wiener index was determined in *Phragmites-G* and *Phragmites-B* in spring. However, *Carex-B* and *Carex-G* showed the lowest Shannon–Wiener index both in spring and autumn.

SOC and DOC contents correlating to vegetation biomass and community biodiversity

Results of regression analysis indicated that SOC had significant positive relationships with above-ground biomass

($R^2 = 0.446$, $p = 0.02$) and below-ground biomass ($R^2 = 0.497$, $p = 0.01$) in spring (Figure 4). Furthermore, SOC was significantly correlated with above-ground biomass ($R^2 = 0.397$, $p = 0.05$) in autumn, but its correlation to below-ground biomass was weak ($R^2 = 0.388$, $p = 0.06$). However, seasonal relationships between SOC and community biodiversity were found to have a contrary tendency by regression analysis (Figure 5). Significant negative relationships were determined between SOC and Margalef indexes ($R^2 = 0.424$, $p = 0.03$) and between SOC and Shannon–Wiener index ($R^2 = 0.488$, $p = 0.01$) in spring, but inverse relationships were found in spite of no statistical significance with $p = 0.10$ and $p = 0.15$ in the autumn, respectively. DOC showed significant positive relationships with above-ground biomass and below-ground biomass both in spring and autumn (Figure 6). Moreover, positive weak relationships were explored between DOC and Margalef index ($R^2 = 0.059$, $p = 0.33$) and between DOC and Shannon–Wiener index ($R^2 = 0.094$, $p = 0.22$) in spring (Figure 7). However, DOC was significantly negatively

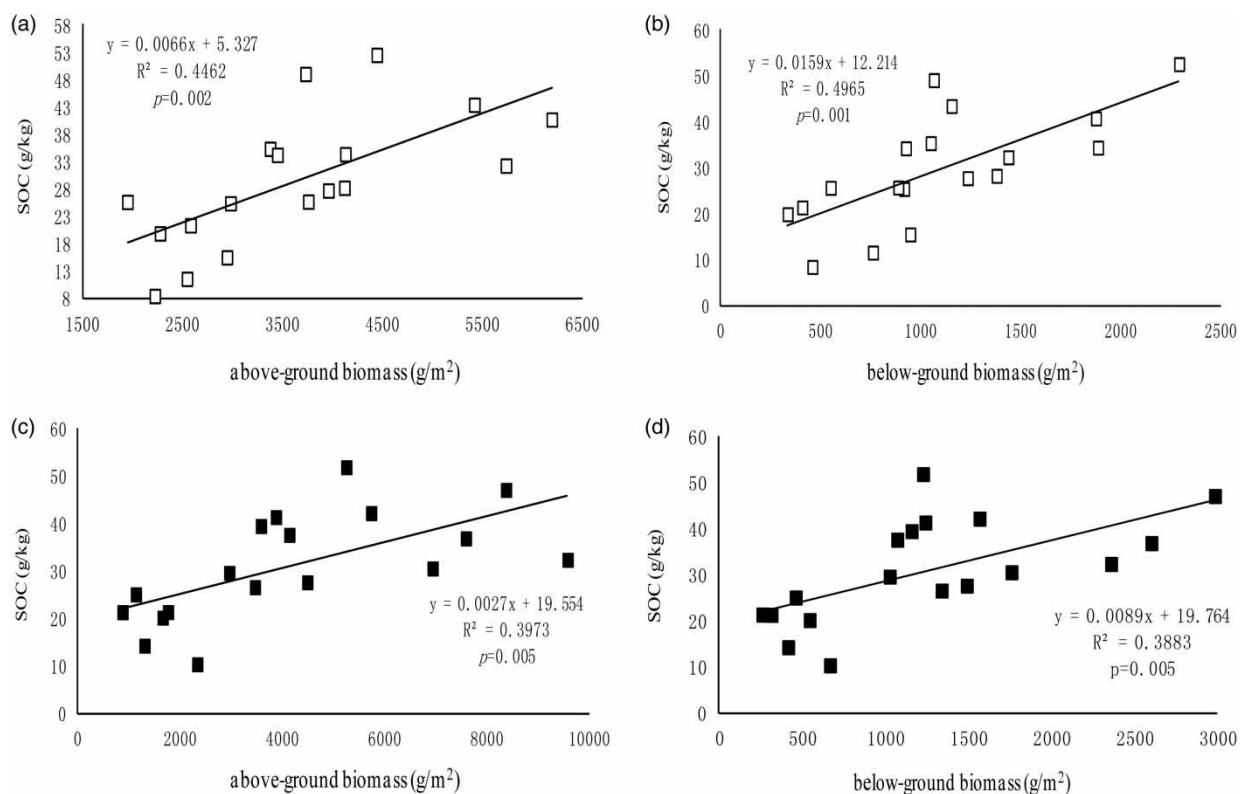


Figure 4 | Seasonal relations between SOC and vegetation biomass in two studied wetlands ((a) and (b) data in spring, (c) and (d) data in autumn, respectively).

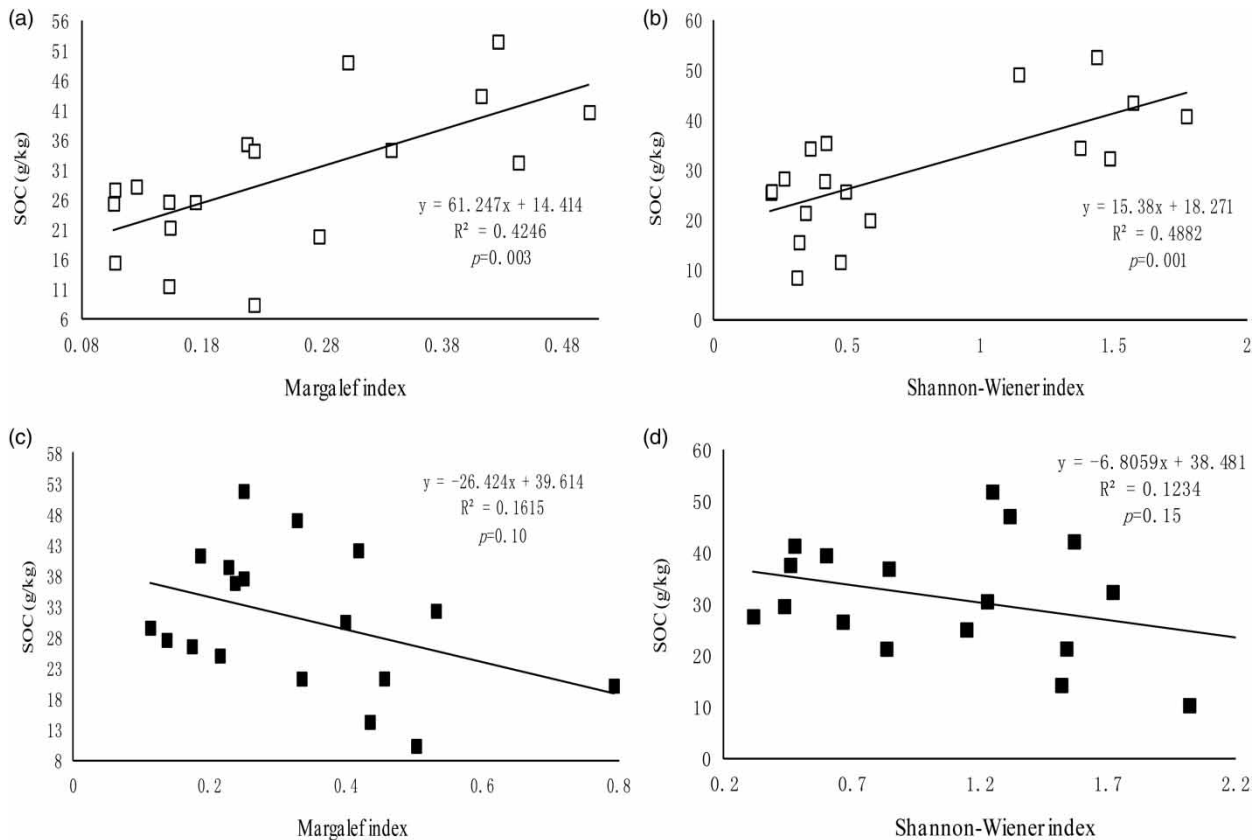


Figure 5 | Seasonal relations between SOC and Margalef index and Shannon–Wiener index in two studied wetlands ((a) and (b) data in spring, (c) and (d) data in autumn, respectively).

correlated to both Margalef indexes ($R^2 = 0.217$, $p = 0.05$) and Shannon–Wiener index ($R^2 = 0.284$, $p = 0.02$) in the autumn.

Relationships between the SOC and related environmental variables

The significant factors (i.e., eigenvalue > 1) loading matrix of PCA are listed in Table 4 and the plot of loadings is presented in Figure 8. Two significant factors were extracted by PCA based on the dataset of BL in spring explaining 76% of the total variance. The first factor accounted for 57% of the total variation and was positively related to SOC (DOC), vegetation biomass, community biodiversity and elevation, and negatively related to gradient. Factor 2 explained 19% of the total variance and was related to coverage, constructive species height, and importance value. Similar to that of BL in spring, two significant factors were extracted by PCA based on the dataset of GD in spring.

The first factor accounted for 57% of the total variance with eigenvalues of 5.7, positively related to SOC, vegetation biomass, community biodiversity and elevation, and negatively related to gradient. Factor 2 related to coverage, constructive species height, and importance value, and explained 20% of the total variance with eigenvalues of 1.9.

As for datasets of BL in autumn, three significant factors accounted for 77% of the total variances. The first factor accounted for 38% of the variance which positively related to SOC, DOC, vegetation biomass, constructive species height and elevation, and negatively related to gradient. Accounting for 28% of the variance, factor 2 was positively related to the Margalef index and Shannon–Wiener index and negatively related to constructive species importance value. Only coverage accounted for the greatest loading for factor 3 that explained 11% of the total variance. Similarly, three significant factors were extracted by PCA based on the dataset of GD in autumn explaining 76% of the total variance. Factor 1 accounted for 35% of the total

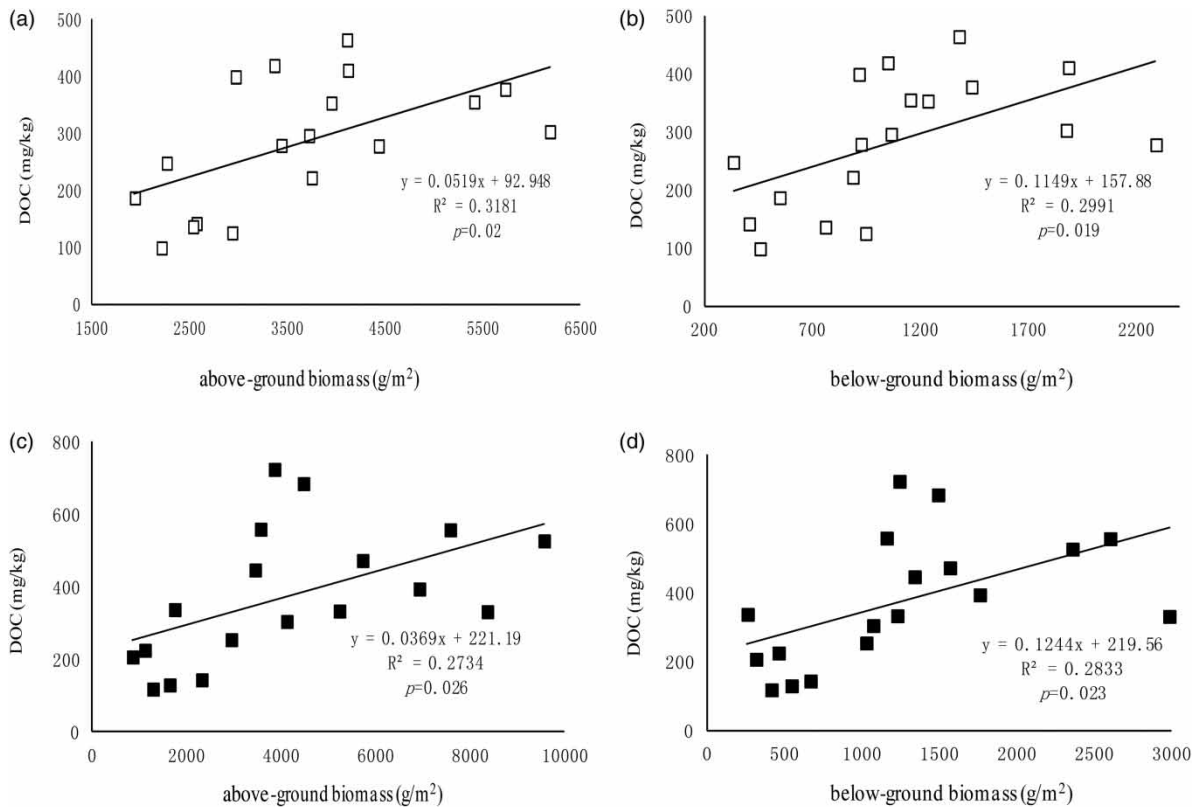


Figure 6 | Seasonal relations between DOC and vegetation biomass in two studied wetlands ((a) and (b) data in spring, (c) and (d) data in autumn, respectively).

variance and was positively related to SOC, vegetation biomass, and elevation, and negatively related to gradient. Factor 2 captured variables of DOC, constructive species importance value, Margalef index, and Shannon–Wiener index, and explained 29% of the total variance. Factor 3 was significantly and positively related only to coverage, accounting for 12% of total variance.

DISCUSSION

Generally, variation of SOC in wetland systems is controlled by the long-term balance between carbon input (e.g., organic matter production and carbon inflows) and output (e.g., decomposition and methanogenesis) (Bellamy et al. 2005; Weishampel et al. 2009). It is argued that the accumulation of organic matter and the soil carbon pool are determined by the decomposition rate rather than by the rate at which organic matter is produced in humid subtropical zones (Malmer et al. 2005; Philippot et al. 2009). The distinct

differences in growth form, amount of aerenchyma, rooting depth, or timing and magnitude of primary production of different plant types have substantial influences on the spatial and temporal heterogeneity of soil carbon in wetlands. In this study, significant differences of SOC content were determined among the three studied vegetation communities, with the highest accumulation in the *Phragmites* community and the lowest in the *Phalaris* community in both spring and autumn. This might be ascribed to the highest biomass of the *Phragmites* community, which could greatly contribute to organic carbon enrichment in surface soil. Accumulating SOC in wetland systems is a complicated process and is affected by multiple factors, among which vegetation is regarded as one of the key factors in the dynamics of sedimentary carbon (Malmer et al. 2005). Moreover, stubbles of *Phragmites* had more complex structures (lignin and cellulose) that are often harder to degrade than those of *Carex* and *Phalaris*. Compared to Ganjiang main-branch delta, BL had a higher content of SOC within the same vegetation type, especially in *Phalaris* with large

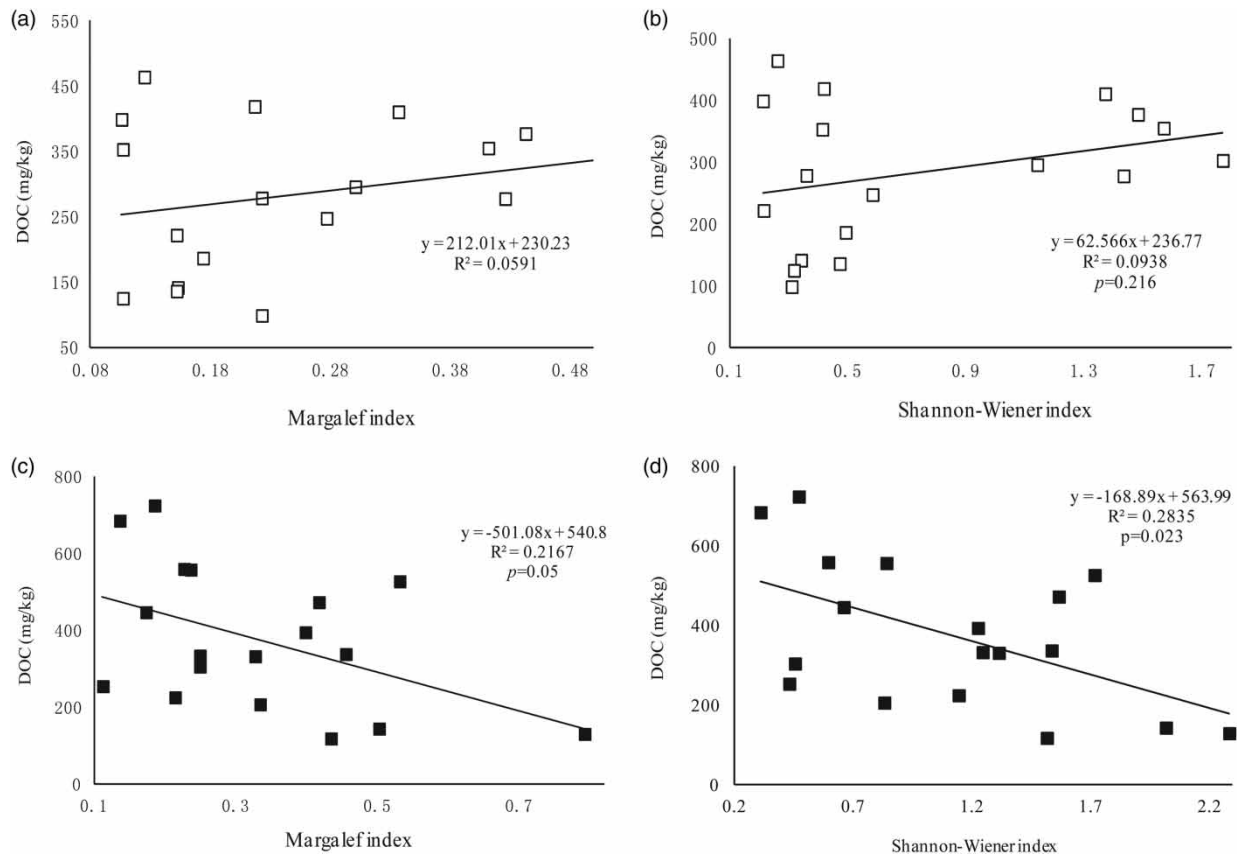


Figure 7 | Seasonal relations between DOC and Margalef index and Shannon–Wiener index in two studied wetlands ((a) and (b) data in spring, (c) and (d) data in autumn, respectively).

differences of SOC between the two typical wetlands. This indicated that dish-shaped pit wetland soil had greater capacity to store carbon. The slow water retreating process in BL induced anaerobic conditions for longer periods, which could constrain decomposition rates of organic matter in soil and, in return, promote organic carbon accumulation. It favors the argument that maintaining traditional sluice control on the flow discharge of dish-shaped pit wetlands could improve pollution retention and food provision for migrant birds (Wang 2005; Jin *et al.* 2011). Furthermore, the unique topography of dish-shaped pit wetland could retain significantly clay particles in the surface soil, which also benefited the increase of SOC content (David & Frank 2007).

DOC in natural wetlands is a complex mixture of compounds and comprises a continuum of organic substances ranging from small molecules to highly polymeric humic substances (Thacker *et al.* 2005; Xiao *et al.* 2010). Many studies

have demonstrated the biochemical processes of DOC production and transformation in wetlands (Catherine *et al.* 2008; Dawson *et al.* 2008). In general, DOC production is influenced by the quantity and quality of organic carbon, and highly correlated to SOC (Evans *et al.* 2005; Song *et al.* 2015). In this study, DOC was correlated with SOC in all vegetation communities with the exception of *Carex*-B, which suggested DOC was highly sensitive to hydrology processing, i.e., flood retention greatly increased DOC content in the *Carex* community. Driven by water level fluctuation, transportation and transformation of organic carbon of the *Carex* community were more complex than those of the *Phragmites* community, in light of DOC being the most active component of carbon pools in wetland and playing an important role in nutrient release and utilization, carbon sequestration, and greenhouse emission (Tranvik *et al.* 2009). Furthermore, in contrast to SOC, greater seasonal variation in DOC was found in the two typical wetlands. DOC contents in autumn were higher

Table 4 | Rotated component matrix of PCA on datasets in two studied typical wetlands both in spring and autumn

Variables	BL		GD		BL			GD		
	Spring				Autumn					
	Factor 1	Factor 2	Factor 1	Factor 2	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3
SOC	0.921*	0.327	0.905*	0.214	0.877*	-0.361	0.215	0.814*	0.331	-0.225
DOC	0.893*	0.445	0.877*	0.326	0.917*	-0.337	0.337	0.572	0.826*	-0.048
Coverage	-0.263	0.916*	-0.305	0.835	0.343	-0.265	0.802*	0.311	0.314	0.873*
Height	-0.217	0.873*	0.177	0.913	0.783*	-0.137	0.281	0.735	-0.353	0.296
Importance value	-0.408	0.782*	-0.336	0.804	0.269	-0.873*	0.467	0.217	-0.819*	0.341
Above-ground biomass	0.864*	-0.331	0.837*	-0.457	0.825*	-0.324	0.115	0.854*	0.421	-0.224
Ground biomass	0.935*	-0.153	0.922*	-0.208	0.906*	-0.463	0.206	0.923*	0.375	-0.069
Margalef index	0.829*	-0.247	-0.759*	-0.371	-0.429	0.892*	0.335	-0.241	-0.813*	-0.132
Shannon–Wiener index	0.753*	-0.386	-0.833*	-0.246	-0.344	0.903*	0.337	-0.305	-0.852*	0.337
Elevation	0.842*	-0.435	0.716*	0.369	0.762*	-0.325	0.242	0.819*	-0.267	0.118
Gradient	-0.732*	0.331	-0.872*	-0.218	-0.769*	0.232	0.431	-0.781*	-0.332	-0.493
Eigenvalues	5.6	2.1	5.7	1.9	3.7	2.6	1.2	3.6	2.8	1.3
% Total variance	57%	19%	58%	20%	38%	27%	11%	35%	29%	12%

*Significance level at $P \leq 0.05$.

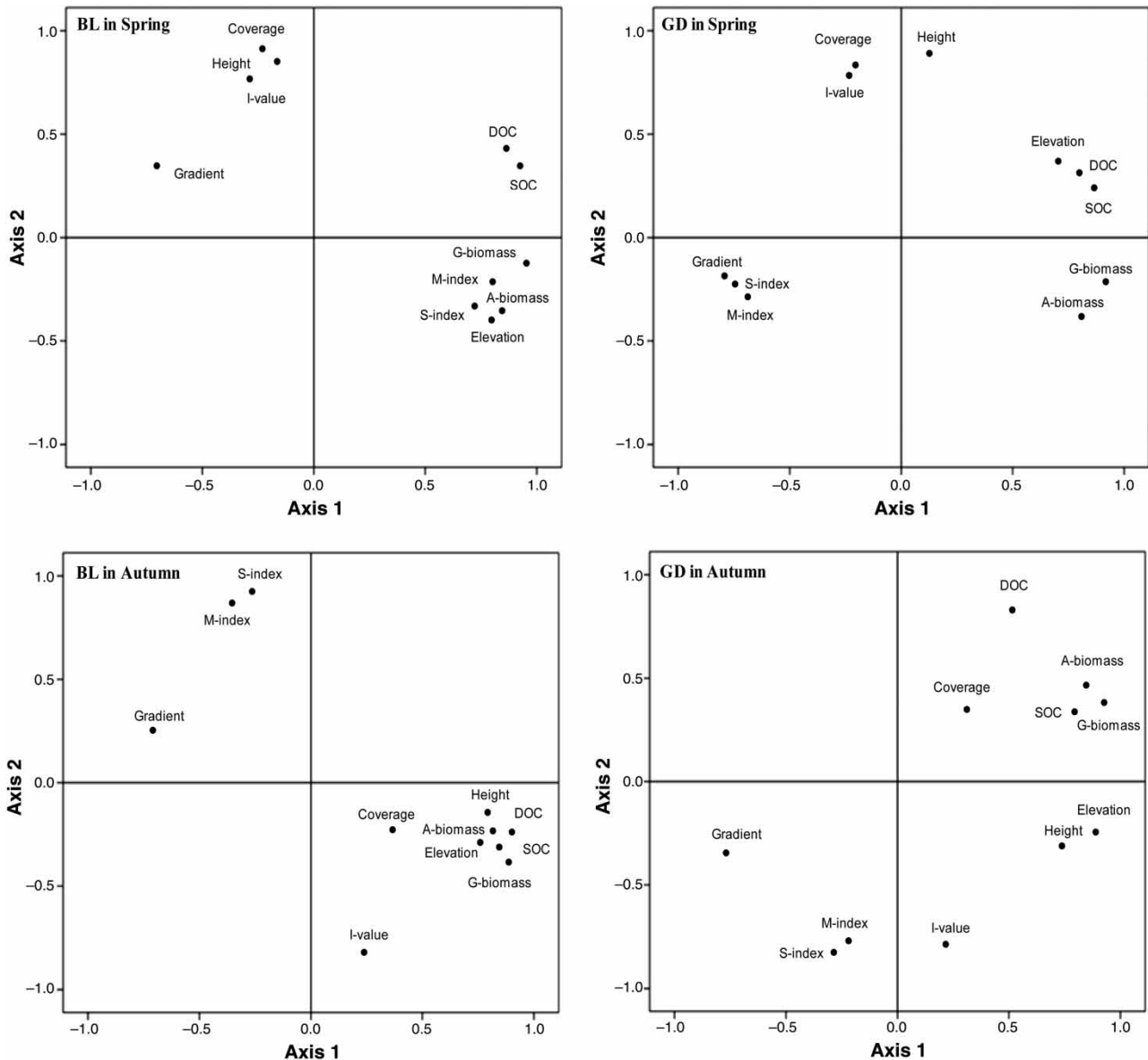


Figure 8 | Plots of factor loadings for each variable of the first two factor axes of BL and GD in spring and autumn data, respectively. I-value, importance value; A-biomass, above-ground biomass; G-biomass, ground biomass; M-index, Margalef index; S-index, Shannon–Wiener index.

than in spring in each vegetation community. Incompletely decomposed organic matter and vegetation litter were the main sources of DOC in wetland surface soil (Mann & Wetzel 1995). Hygrophyte plants distributed on the lake beach (*Phragmites*, *Carex*, and *Phalaris*) died during the flooding period (June to September) in Poyang Lake. The residues of these plants decomposed rapidly when the flood receded, which partially drove the variation of DOC in autumn in the lake (Wang 2005; Ge et al. 2010).

Vegetation directly influences soil carbon accumulation and soil development through above- and below-ground net primary production (Lloyd 2006; Li et al. 2008). Regression analysis in this study found a significant relationship between vegetation biomass and organic carbon in soil both in spring and in autumn, which were positively correlated with the results of PCA. Previous studies had shown that primary production in Poyang Lake was in the range of 500–2,000 g C m² yr⁻¹ (Wang 2005). Several studies

had also found a similar relationship between vegetation biomass and soil microbial biomass, as well as SOC (Wang *et al.* 2010; Yu *et al.* 2011). This suggested that senescent or dead plant biomass may contribute to most of the soil carbon pool in the lake; the below-ground biomass of plants and root exudates especially are directly converted into soil carbon pool by microbial activity. Furthermore, vegetation in Poyang Lake was not only the dominant contributor to soil organic matter accumulation, but also a main resource of organic matter to the lower reaches of the Yangtze River (Dong *et al.* 2012). However, contrasting seasonal tendency had been found in relationships between SOC and community biodiversity by regression analysis. Relationships between plant diversity and SMB are very complex and include positive, negative, hump-shaped, U-shaped, and flat (non-significant) patterns (Gjerde *et al.* 2005; Hirano *et al.* 2012). This could be ascribed to the seasonal variation of biodiversity within typical vegetation communities, especially intensively increasing biodiversity of the *Phalaris* community in autumn. Previous studies demonstrated that vegetation biodiversity strongly related to the elevation in Poyang Lake, rather than nutrient contents in surface soil, although it was argued that soil properties, including content of organic carbon, influenced significantly the plant species richness in some peat wetlands (Lafleur *et al.* 2005; Malmer *et al.* 2005; Wang *et al.* 2016). Generally, wetlands with different hydro-vegetation features have distinct performances in relationships between vegetation community biodiversity and SOC content, which results in difficulty in drawing a universal conclusion.

Both as illustrated by PCA results, SOC and DOC were closely related to elevation, gradient, soil vegetation biomass, and biodiversity. This suggested that, despite great differences in topography, the two typical wetlands were highly consistent in organic matter variation relating to vegetation growth in spring. Although DOC was consistent with SOC in BL, variation of DOC in GD was independent of SOC and vegetation biomass, but negatively related to dominant species importance value and community biodiversity in autumn, which indicated that contents of DOC were more seasonally dynamic, and more sensitive to flood recession in delta wetlands. DOC is the most active component of carbon pools in wetland and plays an important role in

environmental processes, such as nutrient release and utilization, carbon sequestration, greenhouse gas emission, and metal transportation and mobilization (Zweifel 1999; Li *et al.* 2008). It could be assumed that carbon cycling was variable in wetlands with different topography and hydrology features. Furthermore, operation of the Three Gorges Dam strongly influences the water regime of Poyang Lake, especially shortening the flood recession period, which could affect the seasonal dynamic of DOC in the lake (Zhang *et al.* 2012b).

Generally, in water-controlled ecosystems, such as wetlands, plant communities respond to the water level fluctuation (Luo & Xie 2009; Xie *et al.* 2014). Hydrophyte vegetation distributed on the higher beach has a longer growing period, which indicates higher net primary productivity and organic matter input into surface soil, although accompanied by more effective decomposition. Furthermore, it has been well illustrated that organic matter tends to gather in soil micro-aggregates, which are usually accumulated on gentle slopes by erosion (Six *et al.* 2000). This might account for the close and negative relationship between SOC and altitudinal gradient.

CONCLUSIONS

In summary, plant species composition strongly influenced the accumulation of SOC in typical wetlands in Poyang Lake. In contrast to the branch delta, the dish-shaped pit wetland had greater capacity in carbon reserve. Moreover, elevation and gradient also influenced the distributing pattern of organic carbon. In comparison with that of SOC, DOC presented stronger seasonal dynamics with a significant increase in autumn. It is worth noting that a large amount of organic matter accumulates in Poyang Lake from different rivers' watershed each year. However, few studies have demonstrated its relationship with the variations of SOC and DOC in the lake. Future research should focus on the evolution tendency of vegetation communities, especially on the water level fluctuation driven by the interaction of water discharge from the watershed and back flows from the Yangtze River, which directly affected plant growth and vegetation distribution, and in return influenced the dynamics of soil organics carbon.

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