Wetlands Ecol Manage
DOI 10.1007/s11273-014-9396-9

ORIGINAL PAPER

Combined influence of hydrological gradient and edaphic factors on the distribution of macrophyte communities in Dongting Lake wetlands, China

Xinsheng Chen · Xu Li · Yonghong Xie ·
Feng Li · Zhiyong Hou · Jing Zeng

Received: 26 May 2014 / Accepted: 25 November 2014

Abstract Hydrological regime and edaphic factors may operate synergistically to influence plant distribution in wetlands. However, this phenomenon has rarely been examined in freshwater lacustrine wetlands in China. Here, we investigated plant species compositions, hydrological gradients, and soil variables in four dominant plant communities and examined the relationships between plant communities and abiotic factors by using detrended canonical correspondence analysis (DCCA) in wetlands associated with Dongting Lake. The first and second axes of the DCCA ordination explained approximately 52.8 and 26.3 % of the total variance of the species–environment relationship, respectively. Water table depth was the strongest factor related to plant community composition and reflected the spatial distribution of vegetation in wetlands. Water-related soil variables (soil moisture content, bulk density, oxidation–reduction potential, and electrical conductivity) were significantly related to plant distribution. Soil nutrient factors (soil organic matter, total nitrogen, available potassium, and Olsen phosphorus) also played a role in plant distribution. Our findings emphasized the importance of hydrological gradients and related edaphic factors in determining the distribution of vegetation in freshwater wetlands. These findings have implications for conservation of freshwater lacustrine wetlands, which are often subjected to hydrological alteration and nutrient enrichment caused by anthropogenic disturbances and climate change.

Keywords Freshwater wetlands · Species distribution · Emergent macrophytes · Water table · Soil nutrients

Introduction

Freshwater lakes provide a wide variety of ecological services, including flood mitigation, water supply, nutrient retention, and wildlife habitat (Brinson et al. 2002; Shao et al. 2012), and are among the most threatened ecosystems in China because many freshwater lakes in this region have been fragmented and converted to other land uses (Fang et al. 2005; Cui et al. 2013). Because of enhanced awareness of their importance, a series of programs have been implemented to restore the structure and ecological services

---

Xinsheng Chen and Xu Li these authors have contributed equally to this work.

X. Chen · X. Li · Y. Xie (✉) · F. Li · Z. Hou · J. Zeng
Dongting Lake Station for Wetland Ecosystem Research, Institute of Subtropical Agriculture, The Chinese Academy of Sciences, Changsha 410125, Hunan, China
e-mail: yonghongxie@163.com

X. Chen · X. Li · Y. Xie · F. Li · Z. Hou · J. Zeng
Key Laboratory of Agro-ecological Processes in the Subtropical Region, The Chinese Academy of Sciences, Changsha 410125, Hunan, China

of lacustrine wetlands (An et al. 2007; Wang et al. 2012; Bai et al. 2013). Macrophytes, which play an important role in the structure of freshwater lake wetlands, have been targeted for restoration and rehabilitation (Bakker et al. 2013). Although significant efforts have been made, many restoration programs have failed because of a lack of knowledge about the crucial environmental factors required by specific wetland macrophyte communities (Kwon et al. 2007; Bakker et al. 2013).

In freshwater lacustrine wetlands, segregation of macrophyte communities along elevational gradients is commonly observed (Stromberg 2001; Riis and Hawes 2002; Dwire et al. 2004). Spatial variation in hydrological conditions is considered to be a major determining factor in plant species distribution (Silvertown et al. 1999; Riis and Hawes 2002; Vervuren et al. 2003; Luo et al. 2008; Zelnik and Čarni 2008). Along elevational gradients, flood-sensitive species are usually distributed at higher-elevation sites because of their low tolerance to flooding, whereas flood-tolerant species usually occur at lower elevations (Vervuren et al. 2003; Luo et al. 2008).

Despite the importance of hydrological conditions in the distribution of freshwater macrophytes, other evidence has indicated that edaphic factors, such as soil texture and nutrients, play decisive roles in regulating vegetation patterns (Kwon et al. 2007; Lane et al. 2008). In practical terms, the effects of hydrological conditions and soil characteristics on plant growth and distribution are not independent. Variations in hydrology may create gradients in soil variables by controlling the status of soil aeration and associated physical and chemical reactions (Wassen et al. 2002; Kwon et al. 2007). Improvement of the soil environment (e.g., an increase in nutrient supply) may facilitate the acclimation of wetland plants to flooding (Wheeler 1999; Xie et al. 2009). Thus, hydrological conditions and edaphic factors can operate synergistically in determining plant distribution. To date, few studies on wetland soils and hydrology in relation to vegetation have been conducted in Chinese lacustrine wetlands, which are among the ecosystems that are the most threatened by human activities.

The Yangtze River basin contains the densest concentration of freshwater lakes in China and includes 100 shallow lakes with an area of more than 10 km^2 in the middle and lower reaches of the river (Cui et al. 2013). Most of these lakes have been subjected to reclamation or nutrient enrichment in recent decades, which has caused the disappearance or decline of macrophytes (Xu et al. 2006). The abiotic factors that shape these communities are generally unknown; therefore, programs attempting to restore macrophytes appear to lack scientific evidence to support their cause.

The aims of the present study were to examine the relationships between various abiotic factors and the distribution of macrophyte communities in the Dongting Lake wetlands, which are typical lacustrine ecosystems in the Yangtze River basin, with a specific focus on (1) comparing hydrological conditions and soil variables underlying the dominant macrophyte communities along an elevational gradient and (2) clarifying the abiotic factors that are critical to the distribution of macrophyte communities in the Dongting Lake wetlands.

Materials and methods

Study area

Dongting Lake (28°30′–30°20′N, 111°40′–113°10′E), the second largest freshwater lake in China (2,620 km^2), is located in northern Hunan Province in a basin south of the Yangtze River and is connected to the Yangtze by distributary channels. Three major sections of the lake (eastern, southern, and western) have been designated as Wetlands of International Importance by the Ramsar Convention. The mean annual temperature in the study area is 16.4–17 °C, with the coldest temperatures in January (3.9–4.5 °C) and the hottest in July (28.6–29.1 °C). Annual precipitation is 1,382 mm, with more than 60 % falling during the period from April to August. Alluvial soil is the primary soil type in the Dongting Lake wetlands.

The Dongting Lake wetlands are characterized by large seasonal fluctuations in water level (up to 15 m); the wetlands are usually inundated during the period from June to October and exposed from November to the following May. From the water's edge to the uplands, the general pattern of plant zonation consists of a *Phalaris arundinacea* community (designated *Phalaris* hereafter); a *Carex brevicuspis* community (*Carex*); a *Polygonum hydropiper* (*Polygonum*) community, generally embedded within the *Carex* zone;

and a *Miscanthus sacchariflorus* community (*Miscanthus*) (Peng et al. 1984; Xie and Chen 2008).

Field sampling

Nineteen lakeshores containing well-developed wetland vegetation were selected as study sites (Fig. 1). A sampling transect was established on each shore and passed through the plant communities perpendicular to the shoreline. One sampling point was established in the interior of each community type; ecotones containing a mixture of dominant species were avoided. The geographical information of each sampling point was recorded using a hand-held GPS (UniStrong Odin Series, Beijing, China). Some locations did not include all four plant communities; in these areas, one sampling point was established on each shore for each plant community present (*Phalaris*, n = 19; *Carex*, n = 19; *Miscanthus*, n = 15; *Polygonum*, n = 15).

The hydrological regime in wetlands is strongly correlated with elevation of the ground surface and water depth (Urban 2005). Theoretically, if the water level exceeds a certain elevation, vegetation at this elevation can be considered as submerged. Therefore, elevation of the wetlands can represent the duration of submergence in the flooding season (Xie et al. 2014). Hájek et al. (2013) confirmed the usefulness of water-level measurements as a proxy for complex environmental conditions related to the hydrological regime. Therefore, elevation and water table depth were used to represent the water regime in the Dongting Lake wetlands. The accurate elevation of each sampling point was acquired from a digital elevation model (1:10000) of Dongting Lake in 1995, produced by Changjiang Water Resources Commission (Ministry of Water Resources, China), according to the geographical coordinates.

Water table depth and soil variables were collected during December 2008 and January 2009, when the water table is the lowest and most stable (Xie and Chen 2008). A soil profile (80 × 80 × 80 cm) was established at each sampling point. Three soil corers (100 cm^3) were used to collect undisturbed soils from three soil layers (0–20, 20–40, 40–60 cm) for measurement of soil bulk density (SBD). The oxidation–reduction potential (Eh) in each soil layer was measured in situ with a FJA-4 ORP meter (Nanjing Chuan-Di Instrument & Equipment Co., China). An additional soil sample (approximately 1 kg) was collected from each soil layer and taken to the laboratory for measurement of gravimetric soil moisture (GSM), soil organic matter (SOM), electrical

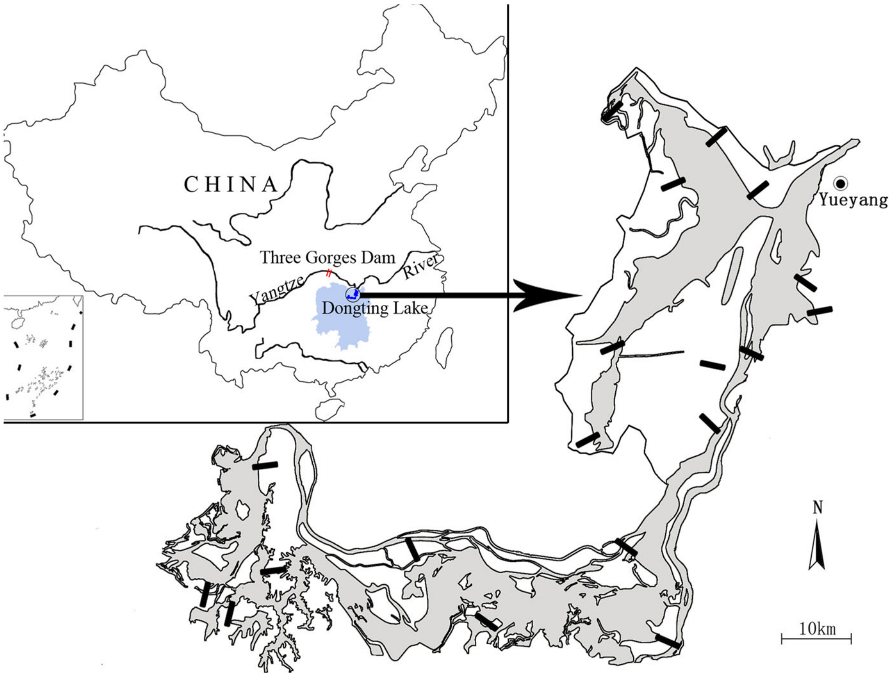

Fig. 1 Locations of the 19 sampled lakeshores in the Dongting Lake wetlands, China

conductivity (EC), total nitrogen (TN), ammonia nitrogen (NH_4–N), total phosphorus (TP), Olsen phosphorus (Olsen-P), total potassium (TK), available potassium (AK), and pH. If necessary, the soil profile was further excavated to reach groundwater. After 2 h (the time required for the water table to stabilize), the water table depth was measured as the distance from the water surface to the ground surface.

In May 2009, when annual species richness and plant biomass were the highest, the following characteristics of the four plant communities were surveyed: species composition, plant biomass, plant density, coverage, and height. One 1-m^2 quadrat was established near each soil sampling point for these measurements. Aboveground shoots within the quadrat were clipped and taken to the laboratory for measurement of aboveground dry biomass, moisture content, and TN and total phosphorous contents. Soil within the quadrat was then excavated to a depth of 20 cm to collect belowground tissues (roots and rhizomes).

Laboratory analysis

Belowground tissue samples were carefully washed such that they were free of soil. Aboveground shoots and belowground tissues were dried in an oven at 60 °C for 48 h to obtain dry weight. Plant biomass was defined as the total dry biomass of aboveground shoots and belowground tissues. Plant moisture content was calculated as ([W−D]/W) × 100 %, where W is the plant fresh weight and D is the plant dry weight. Then, several shoots of dominant species were mixed and ground into fine powder. Samples (approximately 2 g) were digested with H_2SO_4–$HClO_4$ (H_2SO_4:$HClO_4$ ratio of 10:1) and analyzed for plant TN and total phosphorous contents by using colorimetric analysis (Dong 1996).

In total, 204 soil samples were obtained (three depth increments for each soil profile). All procedures for determining soil variables were in accordance with the Chinese national standards (Liu 1996). In the laboratory, each fresh soil sample was divided into two sections; one section was used for GSM and NH_4–N analyses and the other was air-dried in the shade and sieved through a 20- or 60-mesh screen for analysis of the other soil variables. GSM was determined after drying the samples at 105 °C in an oven for 48 h. GSM was calculated as ([W−D]/W) × 100 %, where W is the soil fresh weight and D is the soil dry weight. NH_4–N was extracted with 2 M potassium chloride solution and assayed using a flow injection analyzer (FIAstar 5000, FOSS, Hillerød, Denmark). EC was measured using a conductivity meter (Model DDS-307, Leici, Shanghai, China; soil: distilled water ratio of 1:5); the pH was measured using a pH meter (Model Delta 320, Mettler Toledo, Switzerland; soil: distilled water ratio of 1:2.5). We determined the SOM by wet digestion by using the Walkley–Black method; TN was digested by the micro-Kjeldahl method and measured using a flow injection analyzer (FIAstar 5000); TP was digested by sodium hydroxide and measured colorimetrically using the ascorbic acid reduction method; TK was digested by sodium hydroxide and measured using an atomic absorption spectrometer (Model 932AA, GBC, Melbourne, Australia); Olsen-P was extracted with 0.5 M sodium bicarbonate solution and measured colorimetrically using the ascorbic acid reduction method; AK was extracted with 1 M ammonium acetate solution and measured using an atomic absorption spectrometer. All plant and soil analyses were conducted at the Key Laboratory of Agro-ecological Processes in the Subtropical Region, the Chinese Academy of Sciences.

Data analysis

Species diversity was expressed using the Shannon–Wiener index (Khedr and El-Demerdash 1997) and calculated as:

$$H_i = -\sum P_i Ln P_i$$

where P_i is the importance value of species i, and importance value (%) = (relative height + relative coverage + relative density)/3, relative height = (average height of species i/sum of average height of all species in the plot) × 100 %, relative coverage = (coverage of species i/sum of coverage of all species in the plot) × 100 %, and relative density = (density of species i/sum of density of all species in the plot) × 100 %.

The importance value, rather than the relative abundance, is a better indication of the dominance of a species in a community (He et al. 2004).

The value of each soil variable was calculated from the average value of the three soil layers (0–20, 20–40, 40–60 cm). Differences among abiotic factors and plant community characteristics were analyzed using a general linear model (GLM) in SAS version 8.2 (SAS Institute, Cary, NC, USA). Multiple comparisons of means were performed by Tukey's test at the 0.05 significance level. Data were $\log_{10}$-transformed, if necessary, to reduce the heterogeneity of variances, and homogeneity was tested using Levene's test. The relationships between vegetation and environmental variables were investigated by multivariate analysis. The relationships were best resolved by detrended canonical correspondence analysis (DCCA) based on various iterations. DCCA has advantages over other ordination techniques because it enables a more straightforward interpretation of the figure axes (ter Braak and Šmilauer 2002). The input vegetation data matrix consisted of the importance values of the four dominant species, and the environmental data matrix consisted of water regime and soil variables. DCCA was conducted using CANOCO version 4.5 (Plant Research International, Wageningen, the Netherlands). Species–environment ordination diagrams were prepared with CanoDraw LITE to illustrate the results (Šmilauer 1992).

Results

Characteristics of plant communities

In total, 57 plant species from 21 families and 53 genera were found in the 68 quadrats (Table 1). Thirty-seven species occurred in the *Miscanthus* community, and 22, 24, and 29 species were found in the *Carex*, *Polygonum*, and *Phalaris* communities, respectively (Table 1). Species diversity was significantly lower ($P < 0.05$) in the *Carex* community than in the other three communities, among which there were no significant differences (Table 2). Plant biomass was highest in the *Miscanthus* and lowest in *Polygonum* ($P < 0.05$), with intermediate values in the *Phalaris* and *Carex* communities (Table 2).

Plant moisture content was higher in *Phalaris* and *Polygonum* than in *Miscanthus* and *Carex* ($P < 0.05$, Table 2). Plant TN content was not significantly different among the four dominant macrophytes ($P > 0.05$, Table 2). Plant TP content was higher in *Miscanthus* and *Phalaris* than in *Carex* and *Polygonum* ($P < 0.05$, Table 2).

Abiotic factors in plant communities

The elevation was higher ($P < 0.05$) in *Miscanthus* than in the other three plant communities, among which there were no significant differences (Table 3). Depth to the water table and Eh were highest in *Miscanthus* and lowest in *Phalaris* ($P < 0.05$), with intermediate values in the *Carex* and *Polygonum* communities (Table 3). Values of GSM and EC were higher in the *Phalaris* and *Polygonum* communities than in the *Miscanthus* and *Carex* communities ($P < 0.05$; Table 3). SBD was higher in *Miscanthus* than in the other three plant communities ($P < 0.05$; Table 3); SOM and TN were higher in *Polygonum* than in the other three communities ($P < 0.05$; Table 3); and Olsen-P was higher in *Phalaris* than in the other three communities ($P < 0.05$; Table 3). Values of TK, TP, NH_4–N, and pH did not differ significantly among the four plant communities ($P > 0.05$; Table 3).

Relationship between plant communities and abiotic factors

The first and second axes of the DCCA ordination explained approximately 52.8 and 26.3 % of the total variance of the species–environment relationship, respectively (Table 4). The first axis was positively correlated with water table depth, Eh, and SBD, and negatively correlated with EC, GSM, Olsen-P, and AK (Table 4). The second axis was negatively correlated with SOM and TN (Table 4). Projective sequences of the four plant communities on the DCCA biplot were best represented by the gradient of water table depth (Fig. 2). The *Miscanthus* community was distributed at the higher end of the water table depth continuum, *Carex* and *Polygonum* communities were in the middle, and the *Phalaris* community was at the lower end (Fig. 2).

Discussion

This study revealed that both hydrological gradient and edaphic factors are important in determining plant species distribution in the Dongting Lake wetlands. These results are consistent with studies of several other freshwater wetlands (Stromberg et al. 1996; Dwire et al. 2004; Duval et al. 2012). Hydrological

Table 1 Species observed in the four plant communities and their importance values in Dongting Lake wetlands

Species name	*Miscanthus*	*Carex*	*Polygonum*	*Phalaris*
Alopeculus aequalis Sobol.		0.036 ± 0.011	0.14 ± 0.023	0.084 ± 0.002
Artemisia selengensis Turcz. ex Bess	0.051 ± 0.015		0.021 ± 0.002	0.12 ± 0.018
Astragalus sinicus L.		0.032 ± 0.001	0.14 ± 0.03	0.17 ± 0.034
Avena fatua L.	0.048 ± 0.023		0.092 ± 0.032	
Cardamine hirsuta L.	0.02 ± 0.001	0.15 ± 0.012	0.11 ± 0.007	0.037 ± 0.003
Carex brevicuspis C. B. Clarke	0.21 ± 0.024	0.87 ± 0.074	0.32 ± 0.057	0.02 ± 0.007
Daucus carota L.	0.027 ± 0.002	0.069 ± 0.016	0.03 ± 0.001	0.11 ± 0.006
Echinochloa crusgalli (L.) P. Beauv.			0.018 ± 0.001	0.093 ± 0.008
Eleocharis valleculosa f. *setosa* (Ohwi) Kitag.		0.01 ± 0.002	0.037 ± 0.001	
Euphorbia esula L.	0.028 ± 0.001		0.17 ± 0.037	
Euphorbia helioscopia L.	0.01 ± 0.001		0.062 ± 0.008	
Galium aparine L.	0.041 ± 0.018	0.069 ± 0.026	0.068 ± 0.016	
Gnaphalium uliginosum L.	0.023 ± 0.001			0.092 ± 0.018
Hemisteptia lyrata (Bunge) Fischer & C. A. Meyer	0.047 ± 0.012	0.063 ± 0.007		
Lapsanastrum apogonoides (Maximowicz) Pak & Bremer	0.041 ± 0.016	0.024 ± 0.014		
Leonurus japonicus Houtt.	0.033 ± 0.006		0.018 ± 0.004	0.074 ± 0.005
Mazus pumilus var. pumilus (N. L. Burman) Steenis	0.051 ± 0.004	0.029 ± 0.006		0.122 ± 0.002
Miscanthus sacchariflorus (Maxim.) Hackel	0.50 ± 0.023			
Nasturtium officinale R. Brown		0.056 ± 0.017	0.046 ± 0.012	0.083 ± 0.025
Oenanthe javanica (Blume) de Candolle	0.17 ± 0.037			
Paederia foetida L.	0.011 ± 0.006			
Phalaris arundinacea L.		0.099 ± 0.015	0.13 ± 0.002	0.53 ± 0.026
Phragmites australis (Cav.) Trin. ex Steud.	0.29 ± 0.066			
Poa annua L.		0.10 ± 0.02		
Polygonum posumbu Buch.-Ham. ex D. Don		0.074 ± 0.012	0.021 ± 0.004	
Polygonum hydropiper L.	0.029 ± 0.02	0.14 ± 0.075	0.62 ± 0.079	0.20 ± 0.006
Potentilla fragarioides L.	0.026 ± 0.001	0.047 ± 0.024		0.03 ± 0.012
Ranunculus sceleratus L.	0.076 ± 0.021		0.023 ± 0.002	
Roegneria multiculmis Kitag.	0.036 ± 0.001		0.16 ± 0.018	
Rumex trisetifer Stokes			0.032 ± 0.002	0.036 ± 0.001
Salvia plebeia R. Brown	0.079 ± 0.002		0.027 ± 0.005	0.099 ± 0.024
Saxifraga stolonifera Curtis	0.035 ± 0.023			
Stellaria media (L.) Villars		0.048 ± 0.01	0.045 ± 0.014	0.06 ± 0.008
Trigonotis peduncularis (Trev.) Benth. ex Baker & Moore	0.06 ± 0.012	0.10 ± 0.014		0.017 ± 0.007
Veronica undulate Wallich	0.007 ± 0.001	0.084 ± 0.009	0.046 ± 0.005	
Youngia japonica (L.) Candolle	0.1 ± 0.009			0.017 ± 0.001

Species that occurred in less than 5 % of the quadrats were not shown. Values are mean ± SE

gradient, such as water table depth, was the factor most strongly related to plant species distribution and reflected the spatial distribution of vegetation at our study site. Plants are sensitive to hydrology at a fine scale, and spatial variation in hydrological conditions is thought to cause segregation of species across topographical gradients (Silvertown et al. 1999; Araya et al. 2011; Deng et al. 2013). The water table reflects not only the frequency and duration of flooding, but also drought conditions during the nonflooding season, which is the major growth period for macrophytes in the Dongting Lake wetlands (Xie and Chen 2008;

Table 2 Characteristics of the four plant communities in Dongting Lake wetlands

Variable	*Miscanthus*	*Carex*	*Polygonum*	*Phalaris*
Shannon–Wiener index	0.55 ± 0.09^{a}	0.19 ± 0.08^{b}	0.40 ± 0.10^{a}	0.48 ± 0.11^{a}
Plant biomass (g)	3326.1 ± 227^{a}	2469.3 ± 349^{b}	963.0 ± 268^{c}	1753.4 ± 239^{b}
Plant moisture (%)	61.87 ± 1.78^{b}	66.53 ± 2.03^{b}	71.81 ± 1.57^{a}	77.03 ± 1.03^{a}
Plant total nitrogen (g kg^{-1})	24.08 ± 0.69^{a}	25.88 ± 0.64^{a}	22.04 ± 1.09^{a}	23.47 ± 0.75^{a}
Plant total phosphorus (g kg^{-1})	3.53 ± 0.27^{a}	1.89 ± 0.10^{b}	2.21 ± 0.07^{b}	3.75 ± 0.14^{a}

Different letters indicate significant differences between communities ($P < 0.05$). Values are mean ± SE

Table 3 Hydrological conditions and soil variables in each of the four plant communities in Dongting Lake wetlands. Values are mean ± SE

Variable	Unit	*Miscanthus*	*Carex*	*Polygonum*	*Phalaris*
Elevation	m	26.79 ± 1.40^{a}	25.45 ± 0.75^{b}	25.42 ± 0.99^{b}	24.92 ± 1.45^{b}
WTD	cm	176 ± 22^{a}	80 ± 6^{b}	59 ± 9^{bc}	31 ± 6^{c}
GSM	%	36.79 ± 2.33^{b}	42.70 ± 2.26^{b}	53.42 ± 3.95^{a}	54.37 ± 5.15^{a}
Eh	mV	529 ± 21^{a}	492 ± 44^{ab}	404 ± 43^{b}	244 ± 40^{c}
SBD	g cm^{-3}	1.23 ± 0.02^{a}	1.21 ± 0.03^{ab}	1.11 ± 0.03^{b}	1.13 ± 0.06^{b}
EC	μs cm^{-1}	123.7 ± 10.4^{b}	141.2 ± 11.3^{b}	189.1 ± 16.2^{a}	212.6 ± 27.4^{a}
SOM	%	1.73 ± 0.14^{b}	1.84 ± 0.13^{b}	2.45 ± 0.22^{a}	1.93 ± 0.25^{b}
TN	%	0.11 ± 0.01^{b}	0.13 ± 0.01^{b}	0.17 ± 0.01^{a}	0.13 ± 0.02^{b}
TP	%	0.06 ± 0.00^{a}	0.06 ± 0.00^{a}	0.07 ± 0.00^{a}	0.07 ± 0.01^{a}
TK	%	2.27 ± 0.08^{a}	2.36 ± 0.04^{a}	2.40 ± 0.05^{a}	2.21 ± 0.06^{a}
NH_4–N	mg kg^{-1}	1.84 ± 0.12^{a}	2.11 ± 0.11^{a}	2.65 ± 0.19^{a}	2.70 ± 0.26^{a}
Olsen-P	mg kg^{-1}	9.05 ± 1.51^{b}	9.14 ± 1.29^{b}	10.83 ± 1.91^{b}	16.13 ± 2.85^{a}
AK	mg kg^{-1}	63.64 ± 5.22^{b}	63.66 ± 3.89^{b}	85.67 ± 6.70^{a}	79.36 ± 6.21^{ab}
pH		7.63 ± 0.19^{a}	7.43 ± 0.24^{a}	7.44 ± 0.24^{a}	7.86 ± 0.07^{a}

Different superscript letters indicate significant differences between communities ($\alpha = 0.05$). Values are means ± SEs

WTD water table depth, *GSM* gravimetric soil moisture, *Eh* oxidation–reduction potential, *SBD* soil bulk density, *EC* electrical conductivity, *SOM* soil organic matter, *TN* total nitrogen, *TP* total phosphorus, *TK* total potassium, *NH_4–N* ammonia nitrogen, *Olsen-P* Olsen phosphorus, *AK* available potassium

Chen et al. 2013). Tradeoffs between flooding and drought tolerance are thought to shape the community structure of floodplain meadows (Silvertown et al. 1999; Luo et al. 2008). Physiological evidence indicated that *M. sacchariflorus* has higher drought tolerance and lower flooding tolerance than *C. brevicuspis* and *P. hydropiper*, which might be the mechanism that accounts for the differences in their distribution patterns (Li et al. 2013).

In addition to water table depth, the first axis of the DCCA also reflected changes in soil moisture and aeration status. Soil moisture decreased with increasing depth to the water table, as indicated by the decreasing GSM, while soil aeration improved, as indicated by increasing Eh (Table 3; Fig. 2). Soil moisture and redox conditions affect nutrient availability, water use efficiency, and the concentration of reduced toxic ions and consequently affect plant species composition (Araya et al. 2011; Hájek et al. 2013). With increasing soil moisture, the availability of oxygen may decline (Sajedi et al. 2012). Oxygen deficiency is considered as a major factor that constrains plant growth in flood-prone habitats (Voesenek et al. 2004; Luo et al. 2008). In this study, the gradients of redox potential could well reflect the distribution of plant communities, i.e., *Miscanthus* and *Carex* are distributed in well-aerated sites (Eh > +400 mV), while *Phalaris* is distributed in

Table 4 Summary of detrended canonical correspondence analysis (DCCA) ordinations

Axes	Axis 1	Axis 2
Statistics		
Eigenvalues	0.570	0.222
Species–environment correlations	0.779	0.624
Cumulative variance (%)	52.8	79.1
Correlations		
Total potassium	0.116	–0.244
Available potassium	–0.274*	–0.168
Soil organic matter	–0.142	–0.271*
Total nitrogen	–0.149	–0.281*
Ammonia nitrogen	–0.144	–0.197
Total phosphorus	–0.250	–0.127
Olsen phosphorus	–0.294*	0.211
pH	–0.123	0.104
Electrical conductivity	–0.472***	–0.043
Gravimetric soil moisture	–0.437***	–0.098
Soil bulk density	0.281*	0.127
Oxidation–reduction potential	0.550***	–0.136
Water table depth	0.665***	–0.011
Elevation	0.065	0.007

Percentage variance of species–environment relationships explained by the first two ordination axes

Correlations indicate intra-set correlations of abiotic factors with the first two ordination axes

* $P < 0.05$; *** $P < 0.001$

anaerobic soils (Eh = +244 mV) (Sajedi et al. 2012). Redox values below +300 mV are considered the redox threshold below which root growth is inhibited (Dwire et al. 2006). Only species that have evolved special adaptive strategies such as enhanced porosity and aerenchyma can survive in this low-oxygen condition, similar to *Phalaris* in this study (Voesenek et al. 2004; Qin et al. 2010).

Soil nutrients may play a role in determining plant-species distributions in the Dongting Lake wetlands, as inferred from the second axis of the DCCA biplot, which was significantly correlated with SOM and TN. The importance of soil nutrient gradients in determining plant distribution has been emphasized in several studies (Bedford et al. 1999; Kwon et al. 2007; Huang et al. 2012; Hájek et al. 2013). However, in the present study, NH_4–N, TP, and TK did not differ significantly among the plant communities, and the changes in SOM, Olsen-P, and AK along the water table gradient were not consistent with the patterns of plant community distribution. This result is consistent with findings of a previous study (Duval et al. 2012), which suggests that nutrient gradients are not as critical as the hydrological and soil physical gradients in controlling species distribution. The higher contents of SOM and TN in the *Polygonum* community may indicate the nutrient demand of this species. *Polygonum*

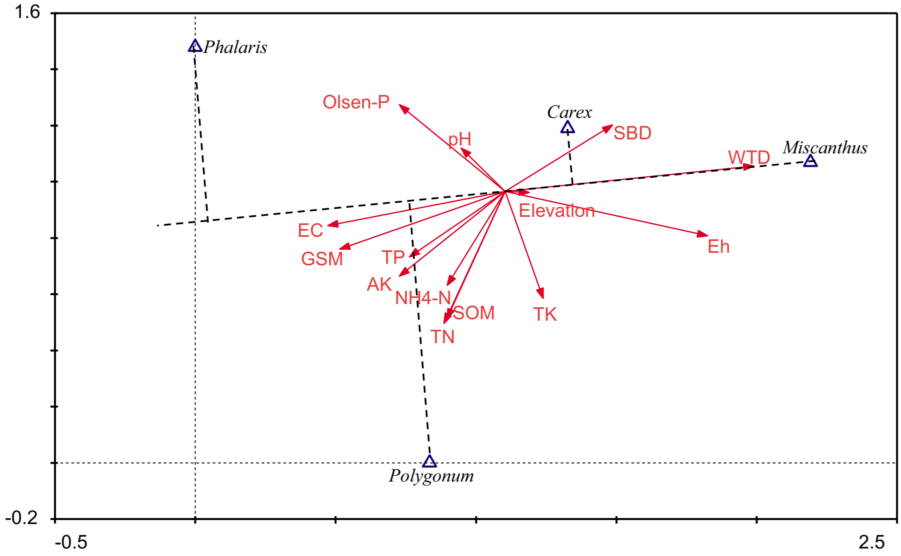

Fig. 2 Detrended canonical correspondence analysis (DCCA) biplots showing relationships between plant communities and abiotic factors in Dongting Lake wetlands. *WTD* water table depth, *GSM* gravimetric soil moisture, *Eh* oxidation–reduction potential, *SBD* soil bulk density, *EC* electrical conductivity, *SOM* soil organic matter, *TN* total nitrogen, *TP* total phosphorus, *TK* total potassium, *NH_4–N* ammonia nitrogen, *Olsen-P* Olsen phosphorus, *AK* available potassium

communities did not form distinct vegetation zones, but were embedded in *C. brevicuspis* zones, which is a potential indication of the importance of spatial heterogeneity of soil nutrients in determining species distribution (Dick and Gilliam 2007).

Apart from water table depth and water-related soil variables, which play decisive roles, soil nutrient factors also play a role in determining the distribution of macrophyte communities in Dongting Lake wetlands. These findings have implications for conservation of freshwater lacustrine wetlands, which frequently experience changes in hydrology and nutrient enrichment due to anthropogenic disturbances and climate change. For example, the belowground water table of the Dongting Lake wetlands has fallen considerably since the opening of Three Gorges Project in 2003 (Jiang et al. 2010), which may result in the characteristic vegetation zones shifting down the elevation gradient (Xie et al. 2011; Tang et al. 2013). Therefore, management of appropriate hydrological conditions is important for the conservation and restoration of Dongting Lake wetland habitats.

Acknowledgments The authors greatly appreciate Dr. W. Wang and Dr. B. Ren for the field assistance they provided and Dr. D. Wang for the identification of plant species. We also thank JJ Qin, YJ Xie, LH Liu, and HL Wang for assisting with soil analysis.

Funding sources This study was supported by the National Key Technology Research and Development Program of China (2014BAC09B03), Basic Work Program of the Ministry of Science and Technology of China (2013FY111800), and the Knowledge Innovation Program of the Chinese Academy of Sciences (ISACX-LYQY-QN-1207).

References

An SQ, Li HB, Guan BH, Zhou CF, Wang ZS, Deng ZF, Zhi YB, Liu YH, Xu C, Fang SB, Jiang JH, Li HL (2007) China's natural wetlands: past problems, current status, and future challenges. Ambio 36:335–342

Araya YN, Silvertown J, Gowing DJ, McConway KJ, Linder HP, Midgley G (2011) A fundamental, eco-hydrological basis for niche segregation in plant communities. New Phytol 189:253–258

Bai JH, Cui BS, Cao HC, Li AN, Zhang BY (2013) Wetland degradation and ecological restoration. Sci World J 2013:1–2

Bakker ES, Sarneel JM, Gulati RD, Liu ZW, van Donk E (2013) Restoring macrophyte diversity in shallow temperate lakes: biotic versus abiotic constraints. Hydrobiologia 710:23–37

Bedford BL, Walbridge MR, Aldous A (1999) Patterns in nutrient availability and plant diversity of temperate North American wetlands. Ecology 80:2151–2169

Brinson MM, Inés A, Várez M (2002) Temperate freshwater wetlands: types, status, and threats. Environ Conserv 29:115–133

Chen XS, Deng ZM, Xie YH, Li F, Hou ZY, Li Xu (2013) Demography of rhizome population of *Carex brevicuspis* (Cyperaceae): a wetland sedge produces both elongated and shortened rhizomes. Nord J Bot 32:251–256

Cui LJ, Gao CJ, Zhao XS, Ma QF, Zhang MY, Li W (2013) Dynamics of the lakes in the middle and lower reaches of the Yangtze River basin, China, since late nineteenth century. Environ Monit Assess 185:4005–4018

Deng ZM, Chen XS, Xie YH, Pan Y, Li F, Hou ZY, Xie YJ (2013) Plasticity of the clonal growth strategy of the wetland sedge *Carex brevicuspis* along an elevational gradient in Dongting Lake wetlands, China. Ann Bot Fenn 50:151–159

Dick DA, Gilliam FS (2007) Spatial heterogeneity and dependence of soils and herbaceous plant communities in adjacent seasonal wetland and pasture sites. Wetlands 27:951–963

Dong M (1996) Survey, observation and analysis of terrestrial communities. China Standards Press, Beijing

Duval TP, Waddington JM, Branfireun BA (2012) Hydrological and biogeochemical controls on plant species distribution within calcareous fens. Ecohydrology 5:73–89

Dwire KA, Kauffman JB, Brookshire ENJ, Baham JE (2004) Plant biomass and species composition along an environmental gradient in montane riparian meadows. Oecologia 139:309–317

Dwire KA, Kauffman JB, Baham JE (2006) Plant species distribution in relation to water-table depth and soil redox potential in montane riparian meadows. Wetlands 26:131–146

Fang JY, Rao S, Zhao SQ (2005) Human-induced long-term changes in the lakes of the Jianghan plain, Central Yangtze. Front Ecol Environ 3:186–192

Hájek M, Hájková P, Kočí M, Jiroušek M, Mikulášková E, Kintrová K (2013) Do we need soil moisture measurements in the vegetation-environment studies in wetlands? J Veg Sci 24:127–137

He XD, Gao YB, Liu HF (2004) Amending of importance value and its implication on classification of *Leymus chinensis* communities. Bull Bot Res 24:466–472 (in Chinese with English abstract)

Huang C, Bai JH, Shao HB, Gao HF, Gao HF, Xiao R, Huang LB, Liu PP (2012) Changes in soil properties before and after wetland degradation in the Yellow River Delta, China. Clean (Weinh) 40:1125–1130

Jiang DW, Huang SC, Zhang YP, Yu DQ (2010) A discussion on the evolution of Dongting Lake based on Geo-environmental remote sensing investigation and monitoring data. Remote Sens Land Resour 86:124–129 (in Chinese with English abstract)

Khedr AHA, El-Demerdash MA (1997) Distribution of aquatic plants in relation to environmental factors in the Nile Delta. Aquat Bot 56:75–86

Kwon GJ, Lee BA, Nam JM (2007) The relationship of vegetation to environmental factors in Wangsuk stream and Gwarim reservoir in Korea: II. Soil environments. Ecol Res 22:75–86

Lane C, Wright SJ, Roncal J, Maschinski J (2008) Characterizing environmental gradients and their influence on vegetation zonation in a subtropical coastal sand dune system. J Coastal Res 24:213–224

Li F, Qin XY, Xie YH, Chen XS, Hu JY, Hou ZY (2013) Physiological mechanisms for plant different distribution patterns: responses of three typical wetland plants to flooding and drought in the Dongting Lake. Liminology 14:71–76

Liu GS (1996) Soil physical and chemical analysis and description of profile. China Standards Press, Beijing

Luo WB, Song FB, Xie YH (2008) Trade-off between tolerance to drought and tolerance to flooding in three wetland plants. Wetlands 28:866–873

Peng D, Yuan Z, Peng G, Tang C, Liao Q (1984) Characteristics and distribution patterns of the vegetation in the Dongting Lake region, Hunan Province. J Central-South For Coll 4:110–119 (in Chinese with English Abstract)

Qin XY, Xie YH, Chen XS (2010) Comparative study on the aerenchyma of four dominant wetland plants in Dongting Lake. J Wuhan Bot Res 28:400–405 (in Chinese with English abstract)

Riis T, Hawes I (2002) Relationships between water level fluctuations and vegetation diversity in shallow water of New Zealand lakes. Aquat Bot 74:133–148

Sajedi T, Prescott CE, Seely B, Lavkulich LM (2012) Relationships among soil moisture, aeration and plant communities in natural and harvested coniferous forests in coastal British Columbia, Canada. J Ecol 100:605–618

Shao HB, Cui BS, Bai JH (2012) Wetland ecology in China. Clean (Weinh) 40:1011–1014

Silvertown JW, Dodd ME, Gowing DJG, Mountford JO (1999) Hydrologically defined niches reveal a basis for species richness in plant communities. Nature 400:61–63

Šmilauer P (1992) CanoDraw 3.0 user's guide version 3.0. Microcomputer Power, Ithaca

Stromberg JC (2001) Restoration of riparian vegetation in the south-western United States: importance of flow regimes and fluvial dynamism. J Arid Environ 49:17–34

Stromberg JC, Tiller R, Richter B (1996) Effects of groundwater decline on riparian vegetation of semiarid regions: the San Pedro River, Arizona. Ecol Appl 6:113–131

Tang Y, Xie YH, Li F, Chen XS (2013) Spatial distribution of emergent herbaceous wetlands in the East Dongting Lake during the last twenty years based on Landsat data. Resour Environ Yangtze Basin 22:1484–1492 (in Chinese with English abstract)

ter Braak CJF, Šmilauer P (2002) CANOCO reference manual and CanoDraw for Windows user's guide, Software for canonical community ordination version 4.5. Microcomputer Power, Ithaca

Urban KE (2005) Oscillating vegetation dynamics in a wet heathland. J Veg Sci 16:111–120

Vervuren PJA, Blom CWPM, de Kroon H (2003) Extreme flooding events on the Rhine and the survival and distribution of riparian plant species. J Ecol 91:135–146

Voesenek LACJ, Rijinders JHGM, Peeters AJM, van de Steeg HM, de Kroon H (2004) Plant hormones regulate fast shoot elongation under water: from genes to communities. Ecology 85:16–27

Wang ZM, Wu JG, Madden M, Mao DH (2012) China's wetlands: conservation plans and policy impacts. Ambio 41:782–786

Wassen MJ, Peeters WHM, Venterink HO (2002) Patterns in vegetation, hydrology, and nutrient availability in an undisturbed river floodplain in Poland. Plant Ecol 165:27–43

Wheeler BD (1999) Water and plants in freshwater wetlands. In: Baird AJ, Wilby RL (eds) Eco-hydrology: plants and water in terrestrial and aquatic environments. Routledge, London

Xie YH, Chen XS (2008) Effects of Three-Gorge project on succession of wetland vegeation in Dongting Lake. Res Agric Mod 29:684–687 (in Chinese with English abstract)

Xie YH, Ren B, Li F (2009) Increased nutrient supply facilitates acclimation to high-water level in the marsh plant *Deyeuxia angustifolia*: the response of root morphology. Aquat Bot 91:1–5

Xie YH, Huang Q, Wang XL (2011) Conservation of wetlands around major lakes in middle-lower Yangtze River Basin. In: Yang GS, Zhu CQ, Jiang ZG (eds) Yangtze conservation and development report. Changjiang Press, Wuhan

Xie YH, Tang Y, Chen XS, Li F, Deng ZM (2014) The impact of Three Gorges Dam on the downstream eco-hydrological environment and vegetation distribution of East Dongting Lake. Ecohydrology. doi:10.1002/eco.1543

Xu QJ, Jin XC, Yan CZ (2006) Macrophyte degradation status and countermeasures in China. Ecol Environ 15:1126–1130 (in Chinese with English abstract)

Zelnik I, Čarni A (2008) Distribution of plant communities, ecological strategy types and diversity along a moisture gradient. Community Ecol 9:1–9