Chin. Geogra. Sci. 2015 Vol. 25 No. 6 pp. 739–756
doi: 10.1007/s11769-015-0774-x

Springer Science Press
www.springerlink.com/content/1002-0063

Effects of Water-table Depth and Soil Moisture on Plant Biomass, Diversity, and Distribution at a Seasonally Flooded Wetland of Poyang Lake, China

XU Xiuli[1, 2], ZHANG Qi[1, 3], TAN Zhiqiang[1, 2], LI Yunliang[1], WANG Xiaolong[1]

(1. *Key Laboratory of Watershed Geographic Sciences*, *Nanjing Institute of Geography and Limnology*, *Chinese Academy of Sciences*, *Nanjing* 210008, *China*; 2. *University of Chinese Academy of Sciences*, *Beijing* 100049, *China*; 3. *Key Laboratory of Poyang Lake Wetland and Watershed Research*, *Ministry of Education*, *Jiangxi Normal University*, *Nanchang* 330000, *China*)

Abstract: Hydrological regime has been widely recognized as one of the major forces determining vegetation distribution in seasonally flooded wetland. Poyang Lake, the largest freshwater lake in China, has been encountering dramatic changes in hydrological conditions in last decade, which greatly influenced the wetland vegetations. To explore the relationships between hydrology and vegetation distribution, water-table depth, soil moisture, species composition, diversity and biomass were measured at a seasonally flooded wetland section at Wucheng National Nature Reserve. Three plant communities, *Artemisia capillaris*, *Phragmites australis* and *Carex cinerascens* communities, were examined which are zonally distributed from upland to lakeshore with decreasing elevation. Canonical correspondence analysis (CCA), spearmen correlation and logistic regression were adopted to analyze the relationships between vegetation characteristics and hydrological variables of water-table depth and soil moisture. Results show that significant hydrological gradient exist along the wetland transect. Water-table demonstrates a seasonal variation and is consistently deepest in *A. capillaris* community (ranging from –0.5 m above ground to +10.3 m below ground), intermediate in *P. australis* community (–2.6 m to +7.8 m) and shallowest in *C. cinerascens* community (–4.5 m to +6.1 m). Soil moisture is lowest and most variable in *A. capillaris* community, highest and least variable in *P. australis* community, and intermediate and moderate variable in *C. cinerascens* community. The CCA ordination indicated that variables of water-table depth and soil moisture are strongly related to community distribution, which explained 81.7% of the vegetation variations. Species diversity indices are significantly positively correlated with soil moisture and negatively correlated with moisture variability, while above- and belowground biomass are positively correlated with moisture. Above- and belowground biomass present Gaussian models along the gradient of average water-table depth in growing season, while species diversity indices show bimodal patterns. The optimal average water-table depths for above- and belowground biomass are 0.8 m and 0.5 m, respectively, and are 2.2 m and 2.4 m for species richness and Shannon-Wiener indices, respectively. Outcomes of this work improved the understandings of the relationship between hydrology and vegetation.

Keywords: water-table depth; soil moisture; species diversity; biomass; Gaussian model; Poyang Lake wetland

Citation: Xu Xiuli, Zhang Qi, Tan Zhiqiang, Li Yunliang, Wang Xiaolong, 2015. Effects of water-table depth and soil moisture on plant biomass, diversity, and distribution at a seasonally flooded wetland of Poyang Lake, China. *Chinese Geographical Science*, 25(6): 739–756. doi: 10.1007/s11769-015-0774-x

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Received date: 2014-08-26; accepted date: 2014-12-29

Foundation item: Under the auspices of National Natural Science Foundation of China (No. 41371062), Collaborative Innovation Center for Major Ecological Security Issues of Jiangxi Province and Monitoring Implementation (No. JXS-EW-00), National Basic Research Program of China (No. 2012CB417003), Science Foundation of Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences (No. NIGLAS2012135001)

Corresponding author: ZHANG Qi. E-mail: qzhang@niglas.ac.cn

1 Introduction

Wetlands are one of the most valuable ecosystems in the world. They provide irreplaceable ecological and economic value in mitigating floods, purifying water, maintaining biodiversity and providing habitats for waterfowl (Ogawa and Male, 1986; Gilliam, 1994; Baschuk *et al*., 2012). Plant communities, as the primary producer, directly determine the structural and functional stability of wetland ecosystems (Rongoei *et al*., 2012; Baattrup-Pedersen *et al*., 2013). Studying the relationships between vegetation distribution and environment factors has been a central issue for decades in ecology, which provided important theoretical information for wetland conservation.

The distribution of vegetation is the result of many environment factors, including climate (Zhang, 2011), topography (Cui *et al*., 2011), hydrology (Auble *et al*., 2005), and soil physiochemical properties (Craft and Richardson, 1997). However, the relative importance of individual factors may vary with different spatial scales and wetland types (Pennings *et al*., 2005; Ji *et al*., 2009). Climate has been regarded as the primary factor in shaping vegetation at continent scale due to geographical differences in precipitation and temperature (Sa *et al*., 2012), while for wetlands at local scale, hydrology process and soil properties have great influences (Castelli *et al*., 2000; Dwire *et al*., 2006). In salt marshes or coastal wetlands, soil salinity has been identified as the dominant factor controlling vegetation distribution, followed by pH, due to severe salt stress (Rogel *et al*., 2000; Ji *et al*., 2009; He *et al*., 2011). In seasonally flooded wetland, flooding is the most typical disturbance that greatly controlled vegetation pattern. Flood pulses cause the plant habitat changing seasonally from terrestrial to aquatic environment that exerts considerable stress on plants (Henszey *et al*., 2004; Pan *et al*., 2012). Crosslé and Brock (2002) suggested that water depth gradient directly determines plant recruitment and survival. Plants inhabiting at specific position along hydrological gradient therefore reflect their flood stress tolerance (Qin *et al*., 2013). Besides, other factors, such as soil nutrient, redox potential and soil texture also influence vegetation growth and distribution (Craft and Richardson, 1997). However, flooding has been mostly considered as the driving force that affects soil physicochemical properties, especially sediment deposition, oxygen availability and chemical reactions, e.g., nutrient forms and transformation (DeBusk and Reddy, 2003; Wang *et al*., 2014). Bai *et al*. (2012) investigated the soil properties along flooding frequency gradient in two seasonally flooded wetlands of Yellow River, and the results showed that the distribution of soil organic content and carbon-nitrogen ratio were significantly correlated with soil moisture. Therefore, hydrologic gradient might have a primary role in shaping vegetation distribution in seasonally flooded freshwater wetland in two ways: directly through water availability and flood stress, and indirectly by changing soil physiochemical properties (Castelli *et al*., 2000; Hammersmark *et al*., 2009). In recent years, wetlands are being severely threatened by altered hydrological processes linked to climate change and intensive human disturbances (Mortsch, 1998; Shafroth *et al*., 2002; Legesse *et al*., 2004). Changes in water regime have been found to alter the soil environment and further cause shifts in species composition and even extinctions of certain species (Leyer, 2005). Consequently, increasing attention has been paid to the vegetation-hydrology relationships in an attempt to better protect and restore wetland ecosystems in a rapidly changing environment (Primack, 2000; Rains *et al*., 2004).

Species diversity and productivity play important roles in maintaining ecosystem stability and biodiversity (Tilman and Downing, 1994; Tilman *et al*., 1996). The influences of hydrological conditions on plant composition, species richness and biomass have been studied most frequently using controlled experiments (Seabloom *et al*., 1998; Crosslé and Brock, 2002; Fraser and Karnezis, 2005). It is undeniable that such controlled experiments have identified the ecological responses of certain species to specific hydrological conditions. However, the results may still need to be verified because the experimental conditions were usually not identical to the field situation. Alternatively, designed field observations along hydrological gradients in typical wetland transects were proved to realistically reflect the field situation and were adopted widely (Asada, 2002; Dwire *et al*., 2006; Booth and Loheide, 2012). Based on transect investigation, the zonation pattern of peatland vegetation was found primarily explained by variables associated with groundwater depth (Asada, 2002). In seasonally flooded riparian wetlands, some studies found both species richness and plant biomass were negatively correlated with water-table depths (Dwire *et al*., 2006; Rongoei *et al*., 2012), while others found species richness presented a unimodal pattern along moisture gradient (Tzialla *et al*., 2006). Besides, the response models of species occurrence probability to soil moisture or water-table depth gradient have also been established (Booth and Loheide, 2012). However, previous studies mainly focused on the vegetation-hydrology correlation relationships or the response curves of individual species to hydrological variables. Limited studies have reported the quantitative distribution patterns of species diversity and biomass along hydrological gradient. Moreover, the changing patterns of vegetation characteristics in relation to hydrology were shown to vary geographically for different ecosystems (Tzialla *et al*., 2006; Zhu *et al*., 2012). The vegetation-hydrology relationships have been performed in peatland, salt marshes and floodplain meadow wetlands with water-table fluctuations less than 4.5 m in American, Europe, and Japan. In view of above summary, further work is needed to examine the characteristics of vegetation-hydrology relationship in wetlands with large seasonal water-level amplitudes.

Poyang Lake, located in the middle reach of the Changjiang (Yangtze) River, is the largest freshwater lake in China. It receives catchment′s runoff from five inflow streams and discharges to the Changjiang River. The lake water level fluctuates seasonally by up to 10 m, which creates vast grass-covered wetlands under periodical inundation (Liu *et al*., 2000). The wetland provides important habitats for millions of migrants and was registered by the UN as an internationally important wetland. However, in the last decade, the lake water regime has been greatly altered due to climate change and the construction of large hydroelectric dams (Min and Zhan, 2012; Zhang *et al*., 2012b). This had brought considerable shifts in plant composition, diversity and biomass, especially for those communities that are sensitive to hydrological variations. It has been noted that under a persistent decline in lake water level, the *Phragmites australis* community has significantly expanded downward and occupied the residence space of the *Carex cinerascens* community, while the *C. cinerascens* community has significantly invaded into the bottomland (Yu *et al*., 2011). The biomass of *P. australis* community has decreased over one half from 1994 to 2009, and the biomass of *Carex* community decreased by approximately two-thirds (Wu *et al*., 2010). Besides, at the upper edge of wetland, vegetation was degraded seriously and some hygrophytes have been replaced by mesophyte (Dronova, *et al*., 2011; Zhou *et al*., 2011). Therefore, a better understanding of the relationships between vegetation characteristics and the changing hydrological conditions has become an urgent and essential issue to be resolved towards a sustainable development of this valuable wetland.

At present, studies on Poyang Lake wetland primarily focused on the hydrological processes (Zhang *et al*., 2012b; Li *et al*., 2014), while the relationships between hydrology condition and vegetation have received little attention. The most common researches were exploring the relationships between distribution areas of vegetation community and the lake water level based on time series Landsat images (Hu *et al*., 2010; Yu *et al*., 2011). Someone also linked the distribution of relative abundance of different communities with inundation duration gradient (Zhang *et al*., 2012a). Most recently, You *et al*. (2013) examined the morphological response of individual species to extreme soil moisture condition. The aforementioned studies have provided knowledge of the relationship between lake level and community distribution. However, to the authors′ best knowledge, the effects of water-table depth and soil moisture on vegetation distribution have not been quantitatively explored so far. In particular, few studies have quantitatively established the distribution pattern of biomass and species diversity in relation to hydrological gradient in Poyang Lake wetlands.

In this study, a typical seasonally flooded wetland transect was selected in Poyang Lake National Nature Reserve (PLNNR) as an experiment site. The site was usually inundated from late May and completely exposed after August. Previous studies representing many seasonally flooded wetland environments through the world have indicated that water-table depth and soil moisture are the dominant factors determining vegetation distribution along topographical gradient, as they directly influence the extent of root zone saturation and flood stress level (Runhaar *et al*., 1997; Hammersmark *et al*., 2009; Mata-González *et al*., 2012). Indeed, other factors, particularly soil physicochemical properties, are also likely to affect vegetation growth. For seasonally flooded wetland, hydrological condition may be indicators of soil chemical reactions and responsible for the nutrient variations through limiting soil oxygen availability (DeBusk and Reddy, 2003; Bai *et al.*, 2012). Therefore, this study, as a first step, aimed to explore the influence of water-table depth and soil moisture on the spatial patterns of biomass and species diversity.

The specific objectives of this paper are to: 1) characterize and compare the spatial-temporal dynamics of water-table depth and soil moisture along the experimental wetland; 2) compare the species composition, diversity and biomass among communities; and 3) relate the hydrological variables to the spatial distribution patterns of vegetation communities, species diversity and biomass. This study is expected to yield an improved understanding of the hydrological effects on vegetation in Poyang Lake wetland, and may provide important support for wetland conservation.

2 Materials and Methods

2.1 Study site

The Poyang Lake wetland has a subtropical humid climate with mean annual precipitation of 1400 mm, nearly 50% of which falls between April and June. Mean annual air temperature is 17℃. It is mainly composed of two types of wetlands: delta and depression wetlands. The delta wetland is the most widely distributed wetland type, which covers approximately 60% of the total natural wetland area (Liu *et al.*, 2000). Meanwhile, the most typical delta wetland is located at the confluence of the Ganjiang River and Xiushui River (Fig. 1a) (Liu *et al.*, 2000).

Our experimental site (116°00′11"E, 29°14′34"N), a seasonally flooded delta wetland transect (A–A′), is just selected at the PLNNR where Xiushui River and Ganjiang River join Poyang Lake (Fig. 1a). It stretches from the upland of Ganjiang River levee to the upper border of mudflats that adjacent to Poyang Lake (the frequently flooded mudflats were not included in the study area), and is approximately 0.8 km in length (Fig. 1b). The topography has an elevation difference of approximately 6 m and the average slope declines from 2% (in upland) to 0.2% (near the lake). The site undergoes alternating wet-dry cycling as floods usually occur in May and recede after August. Approximately 10% of the wetland transect (the upland area) is almost never flooded and 90% is under periodical flooding. Three distinguishing vegetation communities, *Artemisia capillaries*, *Phragmites australis* and *Carex cinerascens* communities are

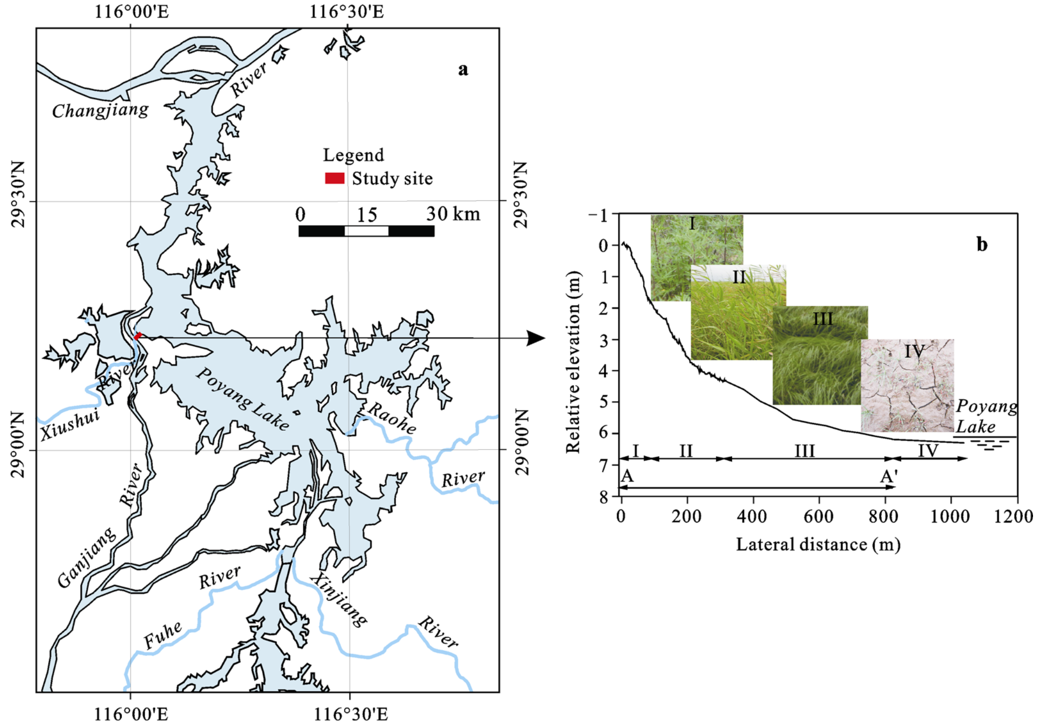

Fig. 1 Location of study site in Poyang Lake (a). A–A′ represents the studied delta wetland transect (b). A is the upland of river levee and A′ is the upper border of lowland mudflats. I, II, III and IV represent *Artemisia capillaris*, *Phragmites australis*, *Carex cinerascens* communities and the mudflats, respectively

distributed zonally along elevation gradient with very obvious borders (Figs. 1b, 2a, 2b). Based on vegetation sampling along wetland transect, spatial variation of the importance values of dominant species were calculated and where dominant species change from one to another was determined as the border between two different communities (Fig. 2c) (Cui *et al*., 2011). The distribution width of each vegetation community and their borders are further measured by topographical survey using the Level Instrument (a point location in *A. capillaris* community was defined as 0 m). *Artemisia capillaries* community is distributed at the upland with lateral distance of 0–70 m, which represents mesophyte ecosystem. It only experienced flooding in high-flow year with less than 1 week. *Phragmites australis* community occurs at the intermediate elevation with lateral distance of 70–290 m, which represents tall-grassland ecosystem. It is usually partially flooded in high water periods for approximately 1–2 months. *Carex cinerascens* community, the most widespread hygrophyte community in Poyang Lake wetland, occupies the lowest elevation with lateral distance of 290–820 m, which represents dense low-grassland ecosystem. This plant zone usually becomes flooded in late May for approximately 3 months and remains completely exposed for the rest of the time. Soil texture is mainly sand in *A. capillaris* community and is silt in *P. australis* and *C. cinerascens* communities based on soil investigation at the middle of each vegetation zone, but the soil particles are finer in *P. australis* community than in *C. cinerascens* community (Table 1).

2.2 Hydrology observation

To measure water-table depth, one well was established in each of the *A. capillaris*, *P. australis* and *C. cinerascens* communities considering the vegetation community distribution and elevation variation. Wells were driven to 15 m below soil surface to reach the groundwater table in dry season. The water levels were recorded automatically by water pressure sensors installed within the wells. A set of three soil moisture sensors were installed at depths of 10, 50 and 100 cm for the *A. capillaris* and *P. australis* community. All data were collected every 10 minutes and recorded hourly from January 2012 to December 2013 (DQC001 and MP406 loggers, LSI-LASTEM Corporation, Italy). In addition, surface soil moisture was also measured manually along the wetland transect every three weeks from March to

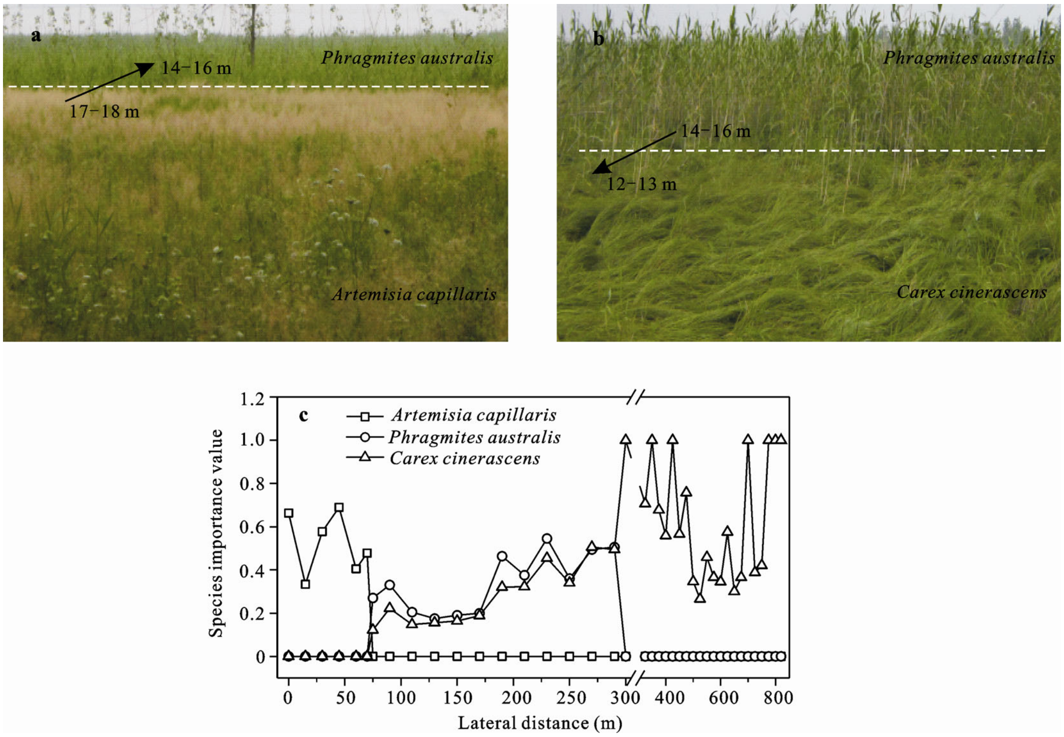

Fig. 2 Distribution of vegetation communities along elevation gradient (12–18 m, Wusong Datum) showing by field photographs (a, b) and importance value of three dominant species along lateral distance (c). The white dash lines are borders between two adjacent communities and the black arrows indicate the direction of slope

Table 1 Soil mechanical analysis results of median grain sizes (D50) sampled at lateral distances of 30 m and 50 m in *Artemisia capillaris* community, 130 m and 250 m in *Phragmites australis* community and 370 m and 520 m in *Carex cinerascens* community

Soil depths (cm)	D50 (μm)		
	A. capillaris community	*P. australis* community	*C. cinerascens* community
0–20	102	60.2	99.8
20–40	272	73.7	90.5
40–60	150	79.2	94.1
60–80	146	77.2	83.6
80–100	165	99.0	92.8
Soil type	Sand	Silt	Silt

Note: sand, D50 > 100 μm; silt, 30 μm ≤ D50 ≤ 100 μm; clay, D50 < 30 μm (refer to Code for Sea Port Hydrology, 2013)

November 2013 at each vegetation sampling plot (see details in Section 2.3). At each time, five measurements from a soil moisture meter (MPKit, ICT Corporation, Australia) were averaged at each plot to obtain a single value. For water-logged area, the saturated soil moisture (equivalent to the porosity) was assigned.

2.3 Vegetation sampling

Two parallel vegetation transects of 820 m in length were set from the uplands to the lakeshore. Along each transect, sampling plots (2 m × 2 m) were arranged at intervals of 30–50 m depending on the widths of the corresponding vegetation belts (Booth and Loheide, 2012), which resulted 6, 12 and 22 plots in the *A. capillaris*, *P. australis* and *C. cinerascens* communities, respectively. Geographic coordinates at each plot was recorded by GPS and the relative elevation was extrapolated from surveyed topography elevation. In April 2013, two quadrats of 0.5 m × 0.5 m were sampled at each sampling plot when most species were thrived and the land was extensively exposed. Each type of species rooted within the quadrat was recorded with average height and percentage coverage (Fang *et al*., 2009). Aboveground biomass was carefully clipped and belowground biomass was excavated to 40 cm depth. All plants were sorted according to species after removing soil particles and separately dried (80℃ for 72 h) to a constant weight.

2.4 Data analysis method

2.4.1 Vegetation and hydrology variables calculation

Species diversity indices are statistical variables to describe the species richness of vegetation community. They were calculated at each sampling quadrat using the following methods (Zhang, 2011):

Species richness index (R):

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

where S is the number of species at each sampling quadrat.

Shannon-Wiener index (H):

$$H = -\sum P_i \ln P_i \tag{2}$$

where P_i is the importance value of species i and calculated by following equation:

$$P_i = (RH_i + RC_i) / 2 \tag{3}$$

where RH_i and RC_i are the relative height and coverage of species i, respectively.

Water-table depth is defined as the distance from visible land surface (0 m) to groundwater table when the land is exposed, and refers to inundation depth when the land is flooded. Hydrology statistical variables from March to November were used to represent growing season hydrology condition and were correlated with the above vegetation characteristics. Growing season average water-table depth (WTD_{ave}) was used and the positive values represent groundwater depth and negative values represent inundation water depth. In order to obtain the estimates of WTD_{ave} at each vegetation sampling plot, interpolation was performed based on the established equation between the WTD_{ave} of the three wells and their corresponding ground elevations ($WTD_{\mathrm{ave}} = -0.94 \times \textit{relative elevation} + 4.65$, $R^2 = 0.999$, $P < 0.001$) (Henszey *et al*., 2004; Booth and Loheide, 2012). Besides, the following soil moisture metrics at each sampling plot were also calculated: growing season average (SWC_{ave}), maximum (SWC_{max}), minimum (SWC_{min}) and coefficient of variation (SWC_{cv}) of the soil water content.

2.4.2 Statistical analysis

Differences in water-table depth and soil moisture among vegetation communities were tested by paired *t*-test (SPSS Statistic, Version 9.0). One-way analysis of variance (ANOVA) followed by the Least Significant Difference (LSD) comparisons were used to evaluate the differences in species richness, Shannon-Wiener index and biomass among vegetation communities. Data were log-transformed ($\lg(x+1)$) to meet the assumptions of normality and homogeneity of variance.

Canonical Correspondence Analysis (CCA) (ter Braak, 1986), a widely used direct gradient analysis, was used to examine the relationship between species distribution and hydrological variables through the CANOCO package. The species important values and the hydrology statistical variables (WTD_{ave}, SWC_{ave}, SWC_{max}, SWC_{min} and SWC_{cv}) for the 40 sampling plots were used as species and environment matrices respectively. Spearman correlation analysis was used to investigate the correlations between aforementioned hydrological variables and the species richness, Shannon-Wiener index, above- and belowground biomass. The changing patterns of biomass and species diversity indices along the WTD_{ave} gradient were established using logistic regression based on Gaussian model in Origin 8.5 (Gause, 1931):

$$y = y_0 + A\exp[-(x-u)^2/2w^2] \tag{4}$$

where the regression parameters of Gaussian model can be interpreted with biological meanings, such as y represents vegetation characteristic indicator; x is the value of environmental factor; u is the optimal environmental value; w is the plant tolerance and 'u + w' is the optimal ecological threshold (ter Braak and Looman, 1986).

3 Results

3.1 Spatio-temporal dynamics of water-table depth and soil moisture

3.1.1 Water-table depth

Water-table showed significantly seasonal variations, and was shallowest from June to August, and deepest from January to February (Fig. 3). The maximum annual water-table depth amplitude was approximately 12 m. Generally, water-table rises rapidly from April to May and started to decline from September. The water-table variation pattern was found to be highly consistent with the changes of Poyang Lake water level (r = –0.99, P < 0.001) (Xu *et al*., 2014). This implied that, at this experimental site, a good hydraulic connection existed between the wetland aquifer and the lake body, and the dynamic of wetland water table was mainly driven by the lake water level.

Strong water-table depth gradient exhibited along the wetland transect (Fig. 3). Water-table depth differed significantly in the three vegetation communities (*A. capillaris* vs *P. australis* community: t = –568.5, P < 0.001; *A. capillaris* vs *C. cinerascens* community: t = –973.8, P < 0.001; *P. australis* vs *C. cinerascens* community: t = –445.8, P < 0.001). The water table was consistently deepest in the *A. capillaris* community (ranging from –0.5 m above ground to +10.3 m below ground), and shallowest in the *C. cinerascens* community (–4.5 m to +6.1 m), and intermediate in the *P. australis* community (–2.6 m to +7.8 m). Water table rose and exposed above ground surface in May, during which time the land was flooded by the surface lake water. Consequently, the *C. cinerascens* community became inundated in early May, and lasted for three to five months with surface water inundation depth of 0–4.5 m. In contrast, the *P. australis* community was only flooded in relatively high lake water level with inundation depth of 0–2.6 m for less than three months, while the *A. capillaris* community was slightly flooded only for a very short time (about one week in 2012).

3.1.2 Soil moisture

Seasonal variation patterns in soil moisture were distinct among the vegetation communities (Fig. 4). In *A. capillaris* community, soil underwent marked seasonal wetting and drying cycles (Fig. 4b). Soil moisture varied seasonally from 2% to 51% and was higher in late

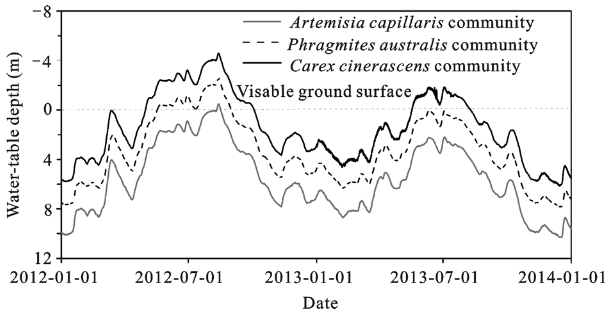

Fig. 3 Water-table depths in the three vegetation communities. 0 m is defined as the soil surface. Positive values refer to groundwater depths (water table is below soil surface) and negative values refer to inundation depths by surface water

spring and summer than in other seasons. However, in *P. australis* community, soil moisture remained at approximately 45% and showed no obvious seasonal variations (the low value at initial phase might not be credible due to the influence of initial installation) (Fig. 4c). In general, the temporal variability of soil moisture was considerably greater in *A. capillaris* community (Coefficient of variance (Cv) = 64%–91%) than in *P. australis* community (Cv = 11%–20%).

Significant differences in soil moisture were observed in *A. capillaris* and *P. australis* communities at all depths (10 cm vs 10 cm depth: $t = -107.6$, $P < 0.001$; 50 cm vs 50 cm depth: $t = -81.0$, $P < 0.001$; 100 cm vs 100 cm depth: $t = -37.8$, $P < 0.001$). In *A. capillaris* community, soil became saturated (~50%) for a short time in summer due to the replenishment of intensified rainfall and elevated groundwater table, but was dry (< 20%) in other seasons (Fig. 4b). However, in *P. australis* community, soil remained fairly wet for almost whole year (Fig. 4c). Besides, the SWC_{ave}, SWC_{max}, and SWC_{min} were all lower in *A. capillaris* community (SWC_{ave} = 7%–15%, SWC_{max} = 25%–34%, SWC_{min} = 1%–3%), were all higher in *P. australis* community (SWC_{ave} = 42%–46%, SWC_{max} = 47%–51%, SWC_{min} = 33%–40%), and the SWC_{ave} and SWC_{max} were higher while the SWC_{min} was relative lower in *C. cinerascens* community (SWC_{ave} = 39%–44%, SWC_{max} = 47%–51%, SWC_{min} = 8%–32%) (Fig. 5). Overall, soil moisture was lowest and most variable in *A. capillaris* community (SWC_{cv} = 68%–116%), highest and least variable in *P. australis* community (SWC_{cv} = 7%–15%), and intermediate and moderate variable (SWC_{cv} = 13%–38%) in *C. cinerascens* community. This indicated that significant different soil water condition existed along delta wetland transect.

The vertical soil moisture gradient was also different among communities (Figs. 4b, 4c). In *A. capillaris* community, the differences in soil moisture among depths were significant (10 cm vs 50 cm depth: $t = -21.40$, $P < 0.001$; 10 cm vs 100 cm depth: $t = -32.3$, $P < 0.001$; 50 cm vs 100 cm depth: $t = -28.7$, $P < 0.001$). Soil moisture at 100 cm was consistently higher than that at 10 and 50 cm. However, in *P. australis* community, the vertical soil moisture gradient was not significantly different (10 cm vs 50 cm depth: $t = -0.03$, $P = 0.973$; 10 cm vs 100 cm depth: $t = -1.6$, $P = 0.098$; 50 cm vs 100 cm depth: $t = -1.97$, $P = 0.049$).

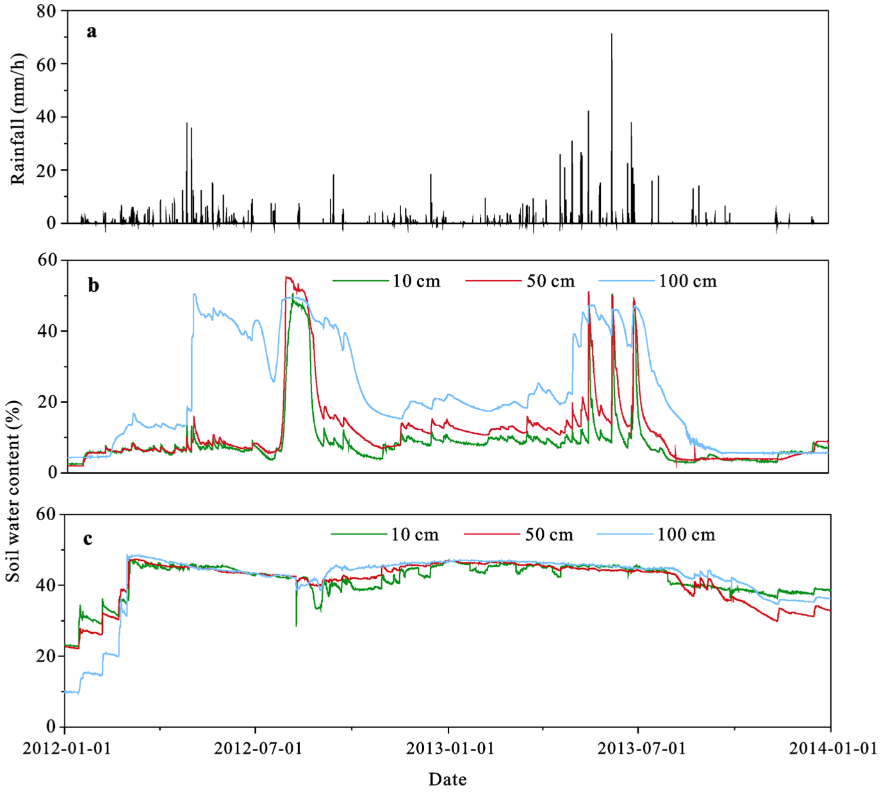

Fig. 4 In suit hourly rainfall (a), continuously observed soil moisture at 10, 50 and 100 cm depth in *A. capillaris* (b) and *P. australis* communities (c)

The differences in soil moisture among vegetation communities may result from a number of factors. For instance, the soil in *P. australis* community may have a higher water holding capacity due to its finer soil particles. It may also be easier for the soil in *P. australis* and *C. cinerascens* communities to be recharged by groundwater since the water table was generally much shallower than that in *A. capillaris* community.

3.2 Vegetation composition, species diversity and biomass

A total of 18 species were discovered (Table 2). Species compositions differed among the *A. capillaris*, *P. australis* and *C. cinerascens* communities. The *A. capillaris* community was dominated by *A. capillaris* and *Cynodon dactylon* with importance values of 0.50 and 0.21, respectively. This community was mainly composed of mesic and xeric plants, and shared few species with the other two communities. The *P. australis* community was mainly composed of emergent plants and hygrophytes. The dominant species of this community were *P. australis*, *C. cinerascens* and *T. lutarioriparia* with importance values of 0.32, 0.31 and 0.16, respectively. In *C. cinerascens* community, *C. cinerascens* was the absolutely dominant species with importance value of 0.67.

Species richness ranged from 1 to 9 species per 0.25m^2 and aboveground biomass varied widely from 11 to 325 g/0.25m^2 (Fig. 6). The relationship between species richness and aboveground biomass showed a skewed unimodal pattern, which can be well described by a significant lognormal distribution equation (R^2 = 0.24, P < 0.001). Species richness first increased with aboveground biomass and reached the maximum with the aboveground biomass of 109 g/0.25m^2 and then decreased with increasing aboveground biomass.

Significant difference in species richness, Shannon-Wiener indices and biomass existed among vegetation communities as shown in Table 3. Species richness and Shannon-Wiener indices were significantly higher than those in *A. capillaris* and *C. cinerascens* communities. However, no significant difference existed between the *A. capillaris* and *C. cinerascens* communities. The highest aboveground biomass was determined in *P. australis* community with values of 61–306 g/0.25m^2, followed by that of *C. cinerascens* (37–209 g/0.25m^2) and *A. capillaris* (11–75 g/0.25m^2) communities. The belowground biomass of *P. australis* community was significantly higher than that of the other two communities with average value of 586.2 g/0.25m^2, while the *A. capillaris* had the lowest belowground biomass with average value of 82.8 g/0.25m^2.

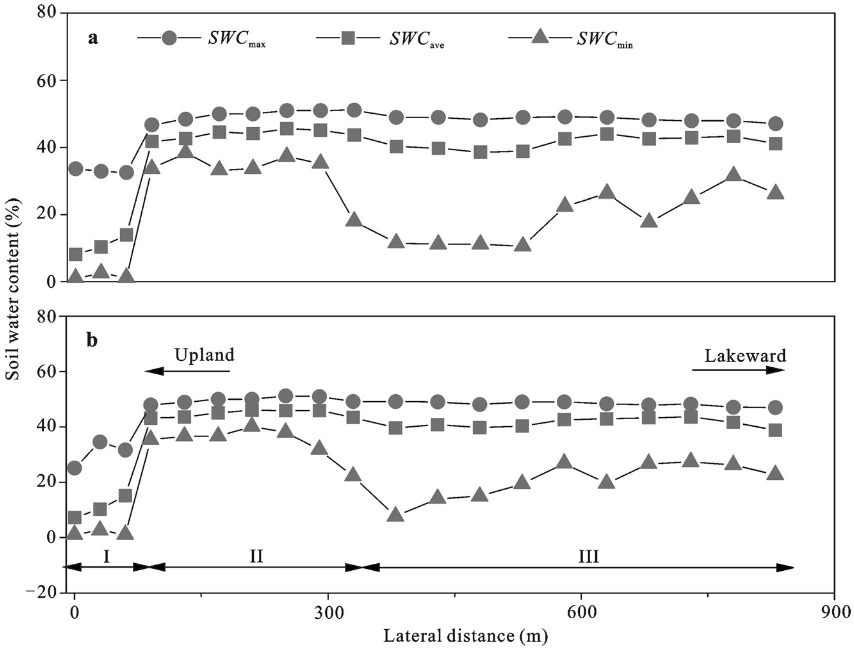

Fig. 5 Spatial variation of soil water content in growing season along two parallel vegetation transects (a) and (b) lying from upland to lakeshore. I, II, III represent the distribution range of *A. capillaris*, *P. australis* and *C. cinerascens* communities, respectively

Table 2 Species importance values and ecotypes for different communities (Mean ± SD)

Species	Ecotype	*A. capillaris* community ($n = 6$)	*P. australis* community ($n = 12$)	*C. cinerascens* community ($n = 22$)
Artemisia capillaris	Xerophyte	0.50 ± 0.18	0	0
Cynodon dactylon	Mesophyte	0.21 ± 0.16	0	0
Eriophorum angustifolium	Mesophyte	0.11 ± 0.07	0	0
Lmperata cylindrical	Xerophyte	0.11 ± 0.12	0	0
Hemarthria altissima	Xerophyte	0.06 ± 0.11	0	0
Astragalus sinicus	Hygrophyte	0	0.02 ± 0.02	0
Alopecurus aequalis	Hygrophyte	0	0.02 ± 0.03	0
Daucus carota	Hygrophyte	0	0.01 ± 0.02	0
Polygonum delicatulum	Hygrophyte	0	0.04 ± 0.03	0
Triarrhena lutarioriparia	Hygrophyte	0	0.16 ± 0.13	0
Phragmites australis	Emergent species	0	0.32 ± 0.12	0
Carex cinerascens	Hygrophyte	0	0.31 ± 0.14	0.67 ± 0.22
Polygonum hydropiper	Hygrophyte	0	0.05 ± 0.05	0.02 ± 0.05
Artemisia selengensis	Hygrophyte	0	0.05 ± 0.04	0.06 ± 0.07
Cardamine lyrata	Hygrophyte	0	0.01 ± 0.02	0.03 ± 0.04
Phalaris arundinacea	Hygrophyte	0	0	0.08 ± 0.20
Eleocharis valleculosa	Emergent species	0	0	0.12 ± 0.16
Polygonum criopolitanum	Hygrophyte	0	0	0.02 ± 0.03

Note: SD is standard deviation

Table 3 Species richness, Shannon-Wiener indices and biomass in different vegetation communities (Mean ± SD)

Vegetation community	Shannon-Wiener index	Species richness index	Aboveground biomass ($g/0.25m^2$)	Belowground biomass ($g/0.25m^2$)
A. capillaris community	0.84 ± 0.27bc	2.7 ± 1.2bc	43.0 ± 13.7c	82.8 ± 11.9c
P. australis community	1.35 ± 0.48a	5.0 ± 2.5a	176.3 ± 82.8a	586.2 ± 418.2a
C. cinerascens community	0.61 ± 0.38c	2.3 ± 1.1c	107.4 ± 54.9b	429.4 ± 394.3b

Note: different letters (a, b, c) following the mean values indicate significant difference among communities within each type of community characteristic at 0.05 level

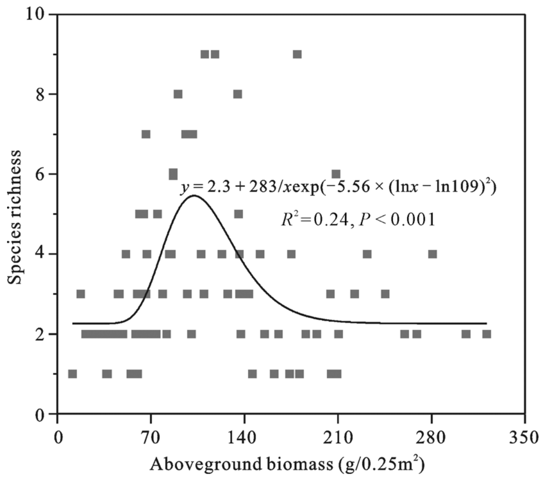

Fig. 6 Relationship between species richness and aboveground biomass. Solid line is the fitted regression equation

3.3 Relationships between vegetation and hydrological variables

3.3.1 Canonical correspondence analysis

The biplot of the CCA clearly separated the three vegetation communities in different zones (Fig. 7). The ordination axes 1 and 2 cumulatively explained 81.7% of the variances in species-environment (Table 4). This revealed that statistical variables associated with water-table depth and soil moisture have already captured the majority of the variations in species distribution. Axis 1 was strongly negatively correlated with the $SWC_{\max}$, SWC_{ave} and $SWC_{\min}$, and was positively correlated with the WTD_{ave} and SWC_{cv}, which mainly represented a decreasing soil moisture condition from left to right. The *A. capillaris* community was distributed at the right part of the biplot with very low soil moisture and was clearly distinguished from the *P. australis* and *C. cinerascens* communities (Fig. 7). Axis 2 was strongly positively correlated with WTD_{ave} and SWC_{min}, which represented a decreasing water-table from bottom to top. The *P. australis* community was clustered at the upper left part of the biplot and was further separated from *C. cinerascens* by its deeper water-table.

3.3.2 Spearman correlations analysis

Species richness and Shannon-Wiener indices were significantly positively correlated with SWC_{min} and negatively correlated with SWC_{cv} (Table 5), indicating that more species occurred where soil moisture is higher and less variable. The two diversity indices also positively correlated with WTD_{ave}, which suggested that inundation might cause a decrease in species richness. In addition, above- and belowground biomass both significantly positively correlated with SWC_{ave} and SWC_{max}. This indicated that higher soil moisture favored biomass accumulation. In contrast, no significant correlations were found among above- and belowground biomass with WTD_{ave}. However, when the sampling sites were divided into two groups ($WTD_{\mathrm{ave}} > 0$ m and $WTD_{\mathrm{ave}} < 0$ m) and studied separately, both above- and belowground biomass were found significantly negatively correlated with WTD_{ave} in group with WTD_{ave} greater than 0 m ($r = -0.86$, $P < 0.001$; $r = -0.93$, $P < 0.001$, respectively) and positively correlated with WTD_{ave} in group with WTD_{ave} less than 0 m ($r = 0.95$, $P < 0.001$; $r = 0.97$, $P < 0.001$, respectively), which implied unimodal patterns between biomass and water-table depth.

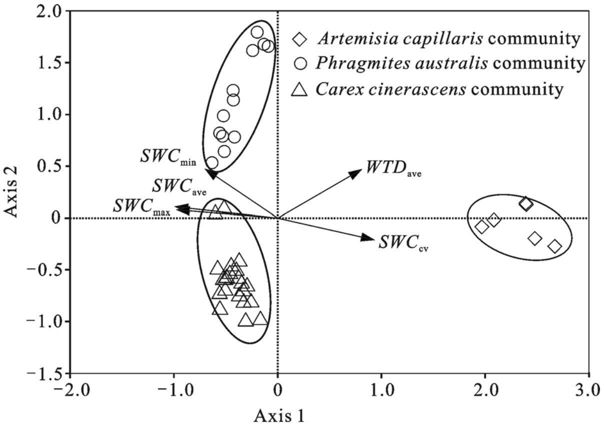

Fig. 7 Canonical correspondence analysis ordination of vegetation sampling plots ($n = 40$) and hydrology variables. SWC_{ave}, SWC_{max}, SWC_{min} and SWC_{cv} represent average, maximum, minimum soil moisture in growing season and the seasonal variation coefficient, respectively. WTD_{ave} represents average water-table depth in growing season

Table 4 Summary of canonical correspondence analysis ordinations

Variable	Axis 1	Axis 2
CCA Eigenvalue	0.968	0.475
Cumulative percentage variance	54.8	81.7
WTD_{ave}	0.803^{**}	0.534^{**}
SWC_{ave}	-0.981^{**}	0.123
SWC_{max}	-0.966^{**}	0.089
SWC_{min}	-0.693^{**}	0.539^{**}
SWC_{cv}	0.923^{**}	−0.239

Notes: **: $P < 0.01$. SWC_{ave}, SWC_{max}, SWC_{min} and SWC_{cv} represent average, maximum, minimum soil moisture in growing season and the seasonal variation coefficient, respectively. WTD_{ave} represents average water-table depth in growing season

Table 5 Spearman correlation coefficients between vegetation characteristics and hydrological variables

Vegetation characteristics	SWC_{ave}	SWC_{max}	SWC_{min}	SWC_{cv}	WTD_{ave}
Species richness index	0.23	0.10	0.36^{*}	-0.39^{*}	0.42^{**}
Shannon-Wiener index	0.21	0.03	0.37^{*}	-0.40^{*}	0.42^{**}
Aboveground biomass	0.51^{**}	0.85^{**}	0.32^{*}	−0.27	0.10
Belowground biomass	0.42^{**}	0.82^{**}	0.18	−0.15	0.08

Notes: *: $P < 0.05$; **: $P < 0.01$. The meanings of SWC_{ave}, SWC_{max}, SWC_{min} and SWC_{cv} and WTD_{ave} are same as in Table 4

3.3.3 Distribution pattern of biomass and species diversity along water-table depth gradient

The changing trends of above- and belowground biomass along the WTD_{ave} gradient were well described by Gaussian models, which captured 87% and 94% of the biomass variations, respectively (Figs. 8a, 8b). The fitted equations demonstrated that the maximum above- and belowground biomass occurred at WTD_{ave} of 0.8 m and 0.5 m, respectively. The optimum WTD_{ave} threshold amplitudes for above- and belowground biomass were [0 m, 1.6 m] and [–0.1 m, 1.1 m], respectively. The species of *C. cinerascens* was found tolerable to a broad range of drying and flooding conditions, which occupied the site with WTD_{ave} ranging widely from –1 m (flooding water depth of 1 m) to 3 m (Fig. 8c). Therefore, the response of *C. cinerascens* to the WTD_{ave} gradient also showed a Gaussian distribution pattern. According to Fig. 8c, the optimum WTD_{ave} of *C. cinerascens* based on total biomass was 0.5 m and the optimum WTD_{ave} threshold of *C. cinerascens* was [–0.1 m, 1.1 m]. In comparison, the species of *P. australis* has adapted to a narrow range of WTD_{ave} ranging from 0.5 m to 3 m (Fig.

8d). The total biomass of *P. australis* increased with the decreasing of WTD_{ave} showing a significantly negative linear correlation relationship. However, the total biomass of *A. capillaris* did not exhibit obvious relationship with WTD_{ave}.

Species richness and Shannon-Wiener indices both presented bimodal patterns along the WTD_{ave} gradient with the first peaks significantly higher than the second one (Fig. 9). The patterns can be well described by two combined Gaussian models, which separately explained 71% and 82% of the variations in species Shannon-Wiener and richness indices. Species richness and Shannon-Wiener indices reached their first peaks at the WTD_{ave} of 2.2 m and 2.4 m, respectively, where the upper part of the *P. australis* community was located, dominated by *T. lutarioriparia*, *P. australis*, *C. cinerascens*, *A. selengensis* and *P. hydropiper*. The second peaks of the two indices both occurred at inundation water depth of 0.6 m (WTD_{ave} = –0.6 m), and the dominant species were *C. cinerascens*, *P. arundinacea*, *E. valleculosa*, *C. lyrata* and *P. criopolitanum*. The troughs of species diversity indices between the two peaks corresponded to vegetation plots with relative higher aboveground biomass (higher than 109 g/0.25m^2) (Figs. 8a, 9), which may be ascribed to competitive exclusion.

4 Discussion

In this study, water-table depth and soil moisture were assumed as the primary factors driving the distribution patterns of vegetation communities, species diversity and biomass along topography in Poyang Lake wetland. Generally, this assumption is valid for floodplain and riparian wetland environments that experience both drought and seasonal inundation (Castelli *et al.*, 2000; Asada, 2002; Tzialla *et al.*, 2006). Indeed, many studies have identified that the remarkable hydrological gradient, typically water-table depth and soil moisture, along topography, elevation, and distance from the river, was the predominant factor determining vegetation distribution in seasonally flooded wetlands (Henszey *et al.*, 2004; Leyer, 2005; Baattrup-Pedersen *et al.*, 2013). For

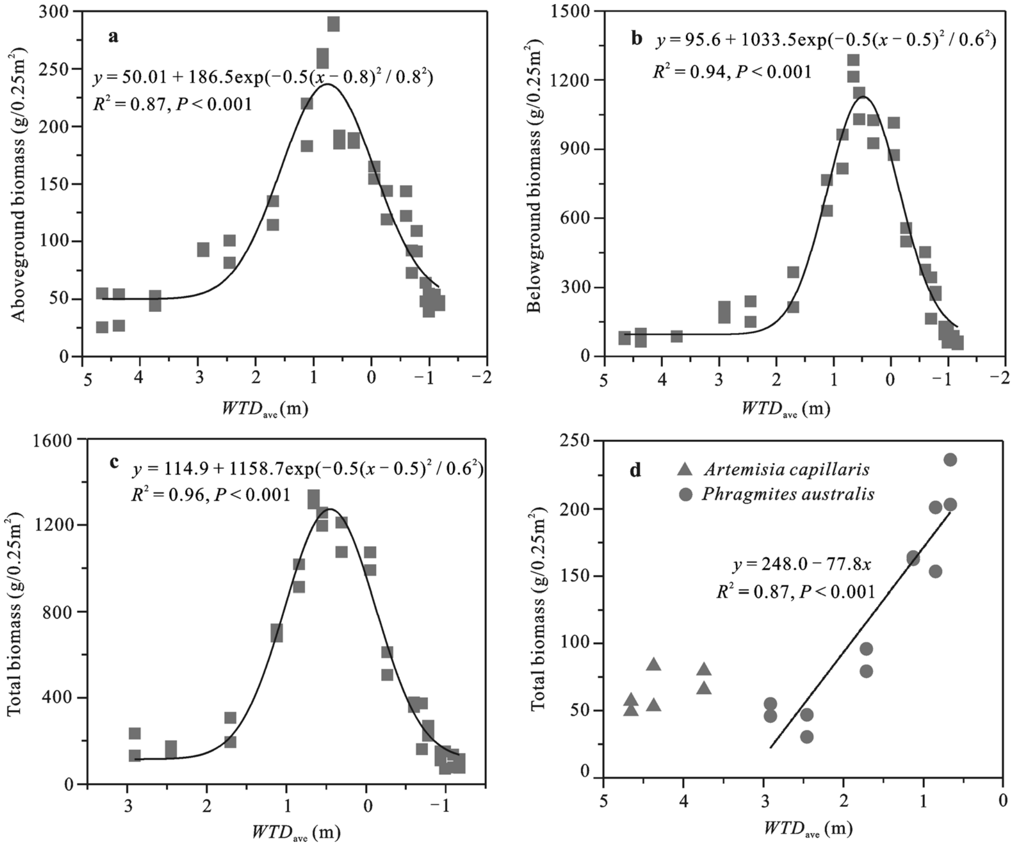

Fig. 8 Relationship between biomass and average water-table depth in growing season (WTD_{ave}). a, aboveground biomass; b, belowground biomass; c, total biomass of *C. cinerascens*; d, total biomass of *A. capillaris* and *P. australis*. Negative values of WTD_{ave} are inundation depths and positive values are groundwater depths. The solid lines are fitted lines

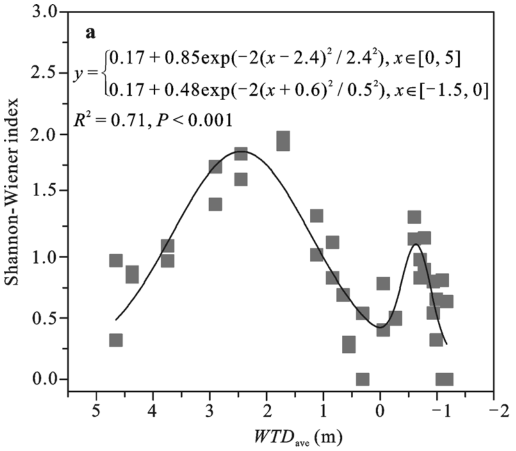

Fig. 9 Distribution patterns of Shannon-Wiener index (a) and species richness index (b) along gradient of average water-table depth in growing season (WTD_{ave}). Negative values of WTD_{ave} are inundation depths and positive values are groundwater depths. The solid lines are fitted lines

Poyang Lake, the seasonally flooded wetland exhibited significant gradients of water-table depth and soil moisture along the lakeside elevation transect (Figs. 3, 4). The results of this study have further supported the assumption and again verified the effectiveness of hydrological variables, as variables of water-table depth and soil moisture have explained 81.7% of the variations in vegetation community distribution (Table 4), 87% and 94% of the variations in above- and belowground biomass, respectively (Figs. 8a, 8b), and 71% and 82% of the variations in Shannon-Wiener and species richness indices, respectively (Fig. 9). However, it should be noted that several other factors including nutrient availability (Craft and Richardson, 1997; Sun *et al.*, 2012), microtopography (Moser *et al.*, 2009; Wolf *et al.*, 2011) and pH (Asada, 2002) also influence the vegetation characteristics distribution. For example, root oxygen availability determines the oxidation-reduction environment and further affects the plant life activity, such as respiration process and nutrient absorption (Castelli *et al.*, 2000; Dwire *et al.*, 2006). These variables may be responsible for the explanation of the remaining variations of vegetation characteristics (approximately 20%) that were not explained in this study. Nevertheless, our results can be regarded as reasonable since they explained approximately 80% of variations in vegetation. On the whole, the observed distribution patterns of vegetation characteristics were formed by the combined effects of a variety of factors with hydrological condition playing a decisive role. To refine the work further, more attention can be paid on the effects of soil physiochemical properties and their interactions with hydrological variables to better explain the vegetation distribution.

This study focused on the three vegetation communities: *A. capillaris*, *P. australis* and *C. cinerascens* at a typical delta wetland transect within the PLNNR. The three communities represent mesophyte, emergent plant, and hygrophyte communities, respectively, which are three major ecotypes in Poyang Lake wetland (Liu *et al.*, 2000). Moreover, the *P. australis* and *C. cinerascens* communities usually exhibit wide zonal patterns in Poyang Lake wetland and cover about 65%–74% of the total wetland area, which are the two largest vegetation types in Poyang Lake wetland (Zhou *et al.*, 2011). It should be further noted that the first consideration in selecting study site was to cover vegetation communities that are sensitive to hydrology changes. Based on previous studies and our field investigation, the three communities selected in this study are usually distributed along elevation gradient. They have been identified as the most sensitive species to hydrological changes, which have exhibited obvious successions and productivity decline in some delta wetlands of the inflow rivers, e.g., the Ganjiang River north-branch and middle-branch delta wetlands (Hu *et al.*, 2010; Wu *et al.*, 2010; Zhang *et al.*, 2012a). Outcomes of this study can increase the understandings of the effects of hydrology changes on these vegetation communities, and also have general implications for the delta wetlands in Poyang Lake.

Species inhabiting at specific elevation along hydrological gradient generally reflect the water requirement and flood tolerance. This was confirmed by our findings in this study. Firstly, the mesophyte and xerophytes (*A. capillaris* community) were only dominated at drought habitat with deep water-table and low soil moisture, while moisture loving hygrophytes (*P. australis* and *C. cinerascens* communities) were distributed at areas where water-table is shallow and soil is almost saturated. Additionally, the *C. cinerascens* community was distributed at area with shallower water-table than the *P. australis* community due to higher flood tolerance. Physiologically controlled experiments showed that *Carex brevicuspis* has a higher flood tolerance and lower drought tolerance compared to *Miscanthus sacchariflorus* (Pan *et al*., 2012; Li *et al*., 2013; Qin *et al*., 2013). Qin *et al*. (2010) found the stem aerenchymatous tissues in *C. cinerascens* were significantly higher than those in *T. lutarioriparia*. Besides, considering the findings that the *P. australis* community preferred the lowest soil moisture variability than the *A. capillaris* community, we may conclude that if drought events were to occur at an increasing frequency, the *P. australis* community is likely to be progressively replaced by the *A. capillaris* community.

In our study, species richness and Shannon-Wiener indices presented bimodal patterns along water-table depth gradient, with largest indices occurring at intermediate to high water-table depth level of 2.2 m and 2.4 m, respectively (Fig. 9), which supported the intermediate disturbance hypothesis that species diversity was supposed to peak at moderate disturbance and environmental stress (Huston, 1979). However, the bimodal patterns are unusual. Most researchers found that species diversity presented a positive or negative linear or unimodal relationship with environment gradient. For example, Rongoei *et al*. (2012) found species richness was negatively correlated with water-table depth in Victoria lake wetland. Dwire *et al*. (2006) reported that species richness positively correlated with water-table amplitude. Sa *et al*. (2012) found that a quadratic polynomial pattern existed between species richness and altitude in alpine ecosystem. Besides, some studies were consistent with ours. Zhu *et al*. (2012) discovered a bimodal pattern of Shannon-Wiener index along groundwater depth gradient in an arid region. Similarly, Xu *et al*. (2011) reported a bimodal pattern along altitude. This indicated that a variety of changing patterns of species diversity existed in different ecosystems. The possible explanation for these distinct shapes is the different range of environmental gradient. A unimodal pattern tends to be more likely found over a long gradient, while a linear pattern is more frequently presented over a short gradient (Leps and Smilauer, 2003). Additionally, many biotic factors (e.g., competition, facilitation and clipping) were also demonstrated to be important drivers of the species richness spatial distribution (Zhang, 2011). A more complicated distribution pattern, such as bimodal shape, can be found under the integrative actions of biotic and abiotic factors.

For the experimental site of this study, the bimodal distribution patterns of species diversity indices are primarily shaped by the combined effect of environmental stresses and species competition. On the one hand, in extremely shallow and deep water-table areas, species richness is limited by severe flood and drought stress. Species richness increases in intermediate water-table area as the environment becomes decent to many species. On the other hand, a high level of biomass also inhibits the species richness. Actually, in this study, relationship between species richness and aboveground biomass demonstrated a lognormal distribution pattern, which is consistent with the previous results that species richness decreased when aboveground biomass exceeded a certain level (Garcia *et al*., 1993; Kassen *et al*., 2000; Mittelbach *et al*., 2001). This is because, at high biomass area, some competitive species always grow fast and exclude the inferior competitive species (Pausas and Austin, 2001). *C. cinerascens*, an intensive clone propagation species, usually produced a completely covered ground in Poyang Lake (Liu *et al*., 2000), which significantly eliminated the survival of other species.

Many studies have found vegetation characteristics shown unimodal distribution patterns along hydrological gradients (Auble *et al*., 2005; Leyer, 2005; Sorrell *et al*., 2012). Tzialla *et al*. (2006) reported that the highest plant productivity was occurred at an intermediate distance from the lake. Luan *et al*. (2013) found the biomass of *Carex lasiocarpa* showed Gaussian models along water-table depth. In this study, above- and belowground biomass and total biomass of *C. cinerascens* along water-table depth gradient all followed Gaussian models (Fig. 8). All the above results illustrate that the maximum biomass usually occurred at the intermediate level over a long hydrological gradient. However, no relationship was found between total biomass of *A. capillaris* and water-table depth. One possible reason may be the small samples size that limited by the narrow distribution width (approximately 70 m) of the *A. capillaris* community. Moreover, this is most likely because the growth of species *A. capillaris* is insensitive to water-table depth changes as the average groundwater table in *A. capillaris* community is deep to 3.7–4.7 m below ground. Given that most roots of the *A. capillaris* are distributed within 40 cm depth, groundwater is not regarded as an important water source for this species. That is to say, the *A. capillaris* has less dependence on groundwater compared with the other two communities. Therefore, it is understandable that no strong relationships exist between biomass of *A. capillaris* and water-table depth. Future studies with more samples at diverse wetlands and the control experiments might give better understandings of their relationships.

Wetlands plants mostly grow in periodic flooding environment; however, they prefer a relatively shallower groundwater table rather than inundation as shown by our results of the optimum water-table depth thresholds for biomass and biomass of *C. cinerascens*. Indeed, even for flood tolerated plants, anoxia stress accompanied by inundation is still the major stress limiting biomass accumulation (Fraser and Karnezis, 2005; Naumburg *et al*., 2005; Rich *et al*., 2011). Besides, many studies have found that flooding usually leads to significantly higher mortality than drying by inhibiting clonal reproduction (Casanova and Brock, 2000; Wang *et al*., 2009). In addition, our results also revealed that an aerated and saturated soil profile with water-table depth of approximately 0.5 m was the optimum growth condition for *C. cinerascens* (Figs. 5, 8c). This finding was supported by a controlled experiment, which suggested that moist to saturated soil was best for *Carex stricta* (Budelsky and Galatowitsch, 2004). The decrease of *C. cinerascens* biomass at water-table depth less than 0.5 m might be primarily caused by root zone anoxic (root depth about 0.3 m).

In recent decade, water regime of Poyang Lake has changed significantly under the influence of climate changes and human activity (Zhang *et al*., 2012b). In future, climate change impacts on Poyang Lake are expected to be manifested with higher frequency of extreme droughts and floods (Ye *et al*., 2011). It may imply that, the seriously polarized water level is likely to increase the variability of soil moisture, which might further result in decrease of vegetation diversity. Additionally, the lake water level in autumn is predicted to decrease by 0.3–1.3 m in response to the climate changes (Ye *et al*., 2011), which might cause a corresponding decline of water table in wetland. Consequently, the mesoxerophytes community may gradually occupy the distribution space of hygrophytes, and the hygrophytes community will spread toward the lake. Since the monitoring period of this study is still short, the data cannot warrant a valid study of the effects of temporal variations of water regime on vegetation characteristics, and this remains a further study when appropriate dataset become available.

5 Conclusions

In this paper, in-suit observations of water-table depth and soil moisture were conducted along a topographic transect at a typical seasonally flooded wetland in Poyang Lake. Vegetation composition, species diversity and biomass were also investigated. Canonical correspondence analysis, spearmen correlation and logistic regression were used to relate vegetation distribution with hydrological variables. The conclusions can be drawn:

Significant water-table depth and soil moisture gradients exist along the lakeshore wetland transect, which determine the vegetation community distribution. Species richness and Shannon-Weiner indices are positively correlated with soil moisture and negatively correlated with moisture variability, while above- and belowground biomass are only positively correlated with soil moisture. The changing trends of above- and belowground biomass along average water-table depth in growing season (WTD_{ave}) can be described by Gaussian models. The maximum above- and belowground biomass occurs at WTD_{ave} of 0.8 and 0.5 m, respectively. The optimum WTD_{ave} thresholds for above- and belowground biomass are [0 m, 1.6 m] and [–0.1 m, 1.1 m], respectively.

The species richness and Shannon-Weiner indices present bimodal patterns along WTD_{ave} gradient with the maximum diversity indices occurring at intermediate to high WTD_{ave} of 2.2 m and 2.4 m, respectively. Besides, the lower species richness and Shannon-Weiner indices were in vegetation either with extreme water-table depth conditions or with large aboveground biomass.

These findings improved knowledge of the spatio-temporal dynamics of water-table depth and soil moisture in Poyang Lake wetland. It also presented the quantitative trends of above- and belowground biomass and species diversity along water-table depth gradient and figure out their optimum water-table depth ranges, which is a significant extension to previous knowledge.

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