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RESEARCH ARTICLE

Effects of water level fluctuations on root architectural and morphological traits of plants in lakeshore areas of three subtropical floodplain lakes in China

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Abstract

Plant roots in lakeshore areas can directly determine the survival of the aboveground plant parts. However, most current studies are focused on the aerial shoots, and less attention has been paid to the functions of the roots. In order to evaluate the effects of water level fluctuations (WLFs) on root architectural and morphological traits of plants in lakeshore areas, field investigations were conducted seasonally in three subtropical floodplain lakes with different types of WLFs. The results showed that both the pH and moisture contents of the soils were significantly different in all seasons among the three lakes, while the total nitrogen and total phosphorus in the soils only showed significant differences in certain seasons. Significant differences were also found in the two architectural trait parameters (root length density and root branching number) and three morphological trait parameters (root tissue density, root surface area, and root volume), all of which (except for root tissue density) were highest in the Dahuchi lake that experiences intermittent WLFs, and lowest in the Chaohu Lake with reservoir-like WLFs. With increasing lakeshore elevation gradients, we found that root length density, root branching number, root surface area, and root volume in the three lakes changed significantly, and all these root trait parameters increased first and then decreased. However, no significant differences were found for the above four root traits in the three lakes over the different seasons. Spearman correlation analyses indicated that both the hydrological and physicochemical factors were strongly correlated with the architectural and morphological root trait parameters, and the duration of submergence (duration) was the most important factor, judging from the correlation coefficients (R). The results of stepwise multiple regression further indicated the duration was the key factor affecting plant root traits. Based on the results of this study, we suggest that the WLFs in reservoir-like lakes should be changed in order to improve the ecological functions of the lakeshore.

Keywords Water level fluctuations · Architectural traits · Morphological traits · Lakeshore elevation · Roots

Introduction

The roles of water level fluctuations (WLFs) in lake ecosystems are gradually being recognized by humans (Coops et al. 2003; Wantzen et al. 2008). Many studies have shown that WLFs are among the most important factors that determine the growth and development of lake plants (Zhang et al. 2015; Yuan et al. 2017), and even small changes in WLFs may result in large shifts in the structure of plant communities (Coops et al. 2003; Magee and Kentula 2005). As major primary producers, lake plants usually respond to periodic or non-periodic changes in water levels through a range of morphological and life history adaptations (Lytle and Poff 2004; Zhang 2013). However, most researchers are focused on the relationships between WLFs and the aboveground parts of lake plants, and less attention has been paid to the roots. The most important reason for this may be that the excavation, washing, and measurement of plant roots are time-consuming and laborious tasks due to the complex spatial configuration of roots.

In addition to providing anchorage, the main function of roots is to absorb limiting nutrients (such as nitrogen and

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phosphorus) and water from the soil (Bardgett et al. 2014). Over the course of evolutionary time, plant roots have developed a series of belowground strategies to obtain these resources and to respond positively to the temporal and spatial variations of their availability (Lambers et al. 2008; Chapman et al. 2012). Changes in architectural and morphological traits are the two main aspects of adaptation to variations in resource availability. The former mainly include rooting depth, root length density, and root branching number, which determine the spatial configuration of the entire root system; the latter mainly include root diameter, root tissue density, and root surface area and volume (Bardgett et al. 2014). At present, there is new evidence to indicate that most plant biomass is under ground, and the roots also have significant effects on ecosystem function (Poorter et al. 2012). Therefore, in order to fully understand the mechanisms of action of WLFs on lake plants, there is a need to carry out systematic studies on the architectural and morphological traits of the roots.

The Yangtze River floodplain is one of the largest floodplains in the world, where hundreds of shallow lakes were freely connected with the Yangtze mainstem (Zhang et al. 2014). However, such river-lake connections were blocked by sluices or embankments for most of the lakes between the 1950s and 1970s, and the natural WLFs in these lakes were altered to various extents (Wang and Dou 1998). According to Zhang (2013), there are three classifications of lake types: WLFs in first lake type are reservoir-like, and include some disconnected lakes. Water levels in these lakes are higher in winter and spring, and low in late spring to early summer, which is opposite to the natural condition (such as Chaohu Lake, Fig. 1a). The WLFs in the other two lake types are intermittent and quasi-natural, respectively. The former includes the lakes or sub-lakes that are only connected to the Yangtze mainstem or Yangtze-connected lakes during the high water level period, and the water level is stable and low in winter and spring (an example is Dahuchi Lake, Fig. 1b). The latter includes all the Yangtze-connected lakes and some disconnected lakes, and the WLFs are similar to the Yangtze mainstem (such as Wuchang Lake, Fig. 1c). In recent years, the effects of WLFs on the aboveground parts of lake plants have been extensively reported in the Yangtze River basin (e.g., Zhang 2013; Zhang et al. 2015; Yuan et al. 2017), but no studies dealing with the belowground parts have been reported to date.

In the present study, three typical lakes (Chaohu Lake, Wuchang Lake, and Dahuchi Lake) with different types of WLFs were selected as the model systems, and plant roots and soils from the shores of these three lakes were collected seasonally. We asked two questions: (1) Are the architectural and morphological root traits significantly different between the three lake types? and (2) What are the most important factors that determine root architectural and morphological traits? We hypothesized that the root traits would be

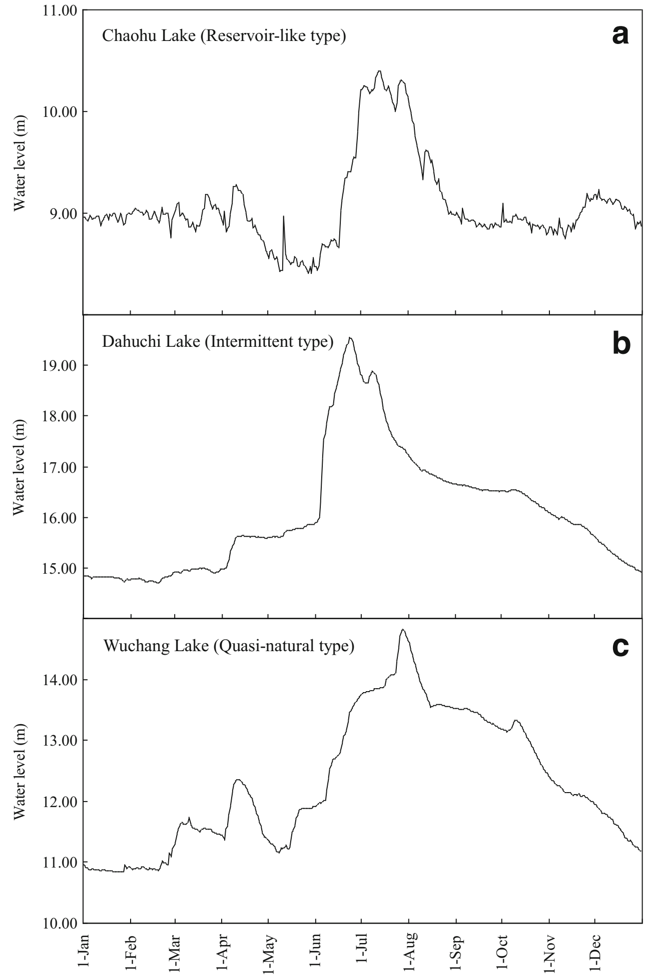

Fig. 1 Water level fluctuations for the three lake types in the normal hydrological year 2015

significantly different in response to the different types of WLFs. The results of this study will not only improve our understanding of the ecological roles of WLFs, but will also have important implications for the management and regulation of lake water levels.

Materials and methods

Study area

The Yangtze River floodplain has a subtropical monsoon climate, and the air temperature and rainfall in this area are obviously different in the different seasons. The Chaohu and Wuchang Lakes are located in the lower reaches of the Yangtze River in Anhui Province (Fig. 2). Historically, the two lakes were connected with the Yangtze mainstem. As a consequence of human disturbance, both Chaohu and Wuchang Lakes were regulated by construction of the Yuxi and Wanhe sluices, respectively. The mean bottom elevation

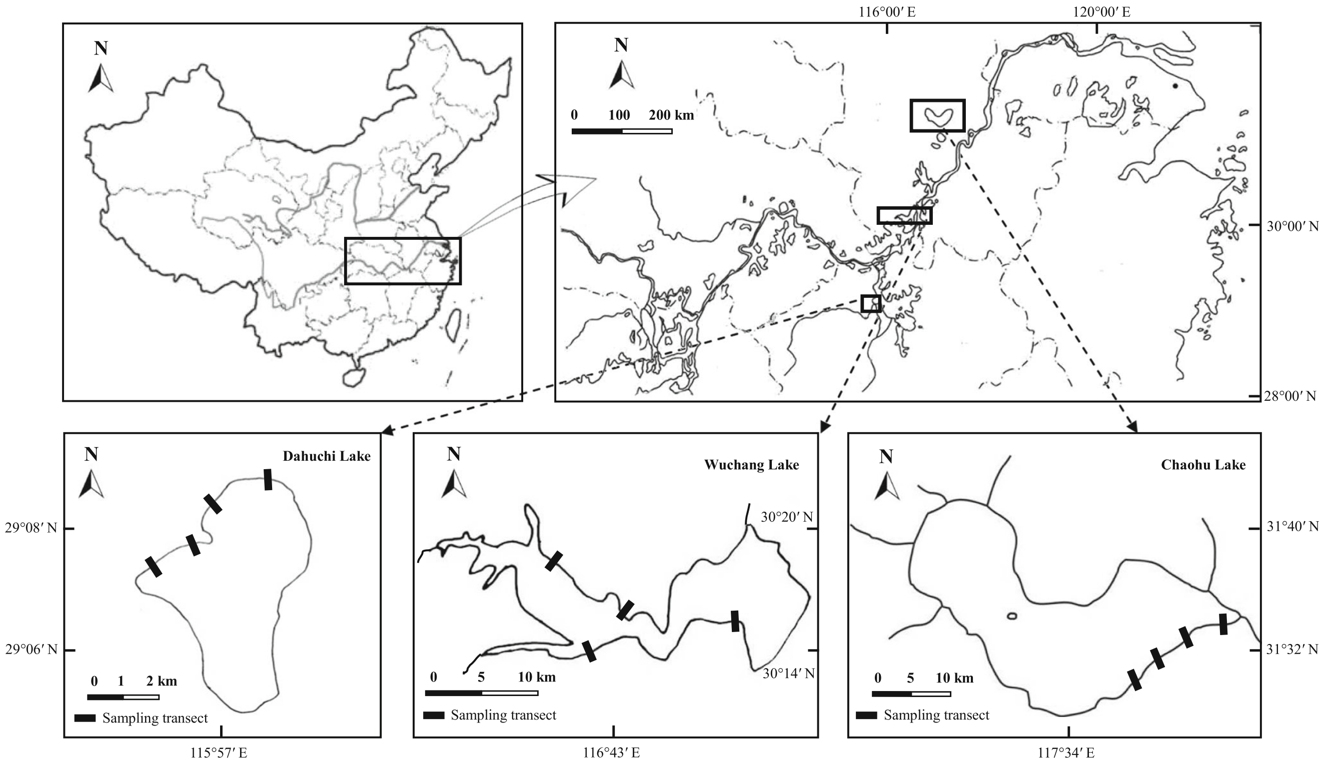

Fig. 2 Location of the sampling transects for Dahuchi, Wuchang, and Chaohu lakes

of Chaohu Lake is 5.0–6.0 m above mean sea level (amsl), and the water level is often maintained at 7.5–8.0 m amsl. Considering the shipping and irrigation, the annual average water level of Chaohu Lake was raised about 1.5 m after the building of the sluice; in addition, to increase the lake's capacity to accept floodwaters, the water levels from late spring to early summer are gradually decreased (Zhang et al. 2014). The mean bottom elevation of Wuchang Lake is 10.0 m amsl, and the water level is often controlled at 11.5 m amsl. The main uses of Wuchang Lake are for aquaculture and flood control, and the WLFs in this lake are similar to the Yangtze mainstem (Zhang et al. 2016). Dahuchi Lake is a sub-lake of Poyang Lake with a mean bottom elevation of 14.67 m amsl, and Dahuchi is only connected to Poyang Lake for about 2 months during the summer high water level period. After that, the water levels are low and stable with a mean water depth of less than 1.0 m. The other limnological variables of the three lakes are given in Table 1.

Field investigations

Field investigations of plant roots and soil physicochemical parameters were conducted in the three lakes in April, August, and November of 2016 and February of 2017. Four transects without artificial embankments, grazing, farming, or other human disturbances were selected for each lake (Fig. 2). At each transect, five sites were set perpendicular to the lakeshore from the mean annual lowest water level to the mean annual highest water level, and were numbered I, II, III, IV, and V in sequence. In order to improve the comparability of the data, the elevation differences were equal between any two adjacent sites in each transect. Because the lakeshore vegetation in the three lakes can be easily classified into different layers, and the distribution of plants in each layer was relatively uniform (Zhang 2013), the plant roots in each site were randomly collected twice using a portable root-soil core sampler (4.0 cm diameter with a depth of 17 cm). The samples were washed carefully in a filtering nylon sieve (150 μm mesh). Roots were then scanned at a resolution of 300 dpi using a scanner (EPSON i800 plus), and the images were analyzed using WinRHIZO software (Regent Instruments Canada Inc., Ottawa, Canada) to determine the root length, volume, surface area, and the branching number of roots from each site. After that, the roots were dried in an oven at 80 °C for 3 days and weighed with an electronic balance. Three soil samples from the top 17 cm were also collected from each site, and the samples were mixed to form a composite sample. In each composite sample, the pH and soil moisture content (MC) were measured by the potentiometric method and the oven-drying method, respectively; the organic matter content (OM) was measured by the $K_2Cr_2O_7$ titration method; total nitrogen (TN) and total phosphorus (TP) contents were measured using the Kjeldahl method and molybdenum blue colorimetry, respectively (Lu 2000).

Table 1 Limnological variables for the three lakes in the Yangtze River floodplain in China

	Chaohu Lake (Reservoir-like type)	Dahuchi Lake (Intermittent type)	Wuchang Lake (Quasi-natural type)
Area (km^2)	769.6	30.0	100.5
Mean water depth (m)	2.69	0.70	3.43
Maximum water depth (m)	3.77	4.43	4.31
Annual precipitation (mm)	995.7	1600.0	1299.6
Annual air temperature (°C)	16.1	17.2	16.5
Recharge coefficient of lake	12.0	–	10.8
Catchment area (km^2)	9258.0	–	1083.7
Volume (m^3)	20.70×10^8	–	3.45×10^8

Data are from Wang and Dou (1998) and Zhang (2013)

Data analyses

The environmental factors used in the analyses were divided into two groups; the physicochemical parameters included pH, MC, OM, TP, and TN, and the hydrological parameters included the amplitude of the WLFs (Amplitude), the duration of submergence (duration), the frequency of submergence (frequency), and the mean submergence depth (depth). Amplitude was defined as the difference between the highest and lowest water levels within a year; the duration was calculated as the sum of number of days that the site was submerged; the frequency was the number of times the site was submerged (Zhang et al. 2014). The depth was calculated as the mean values of the differences between daily water level and the elevation of the site. Hydrological data from 2012 to 2016 were used to determine the mean annual lowest and highest water levels, and the hydrological data from 2016 was used to calculate the four hydrological parameters in this study. The water level data for Poyang Lake was from the Jiangxi Poyang Lake National Nature Reserve, and the data for Wuchang and Chaohu Lakes was from the flood and drought information network of Anhui Province (http://61.191.22.157/Default.aspx).

The root architectural traits used in this study included root length density (RLD) and root branching number (RBN), and the morphological traits included average root diameter (RD), root tissue density (RTD), root surface area (RSA), and root volume (RV). These parameters were calculated using the following equations:

$$\begin{aligned}
\text{RLD} &= \text{Total root length}/\text{Vsoil};\\
\text{RBN} &= \text{Total root branching number}/\text{Vsoil};\\
\text{RD} &= \text{Total root surface area}/\text{Total root length};\\
\text{RTD} &= \text{Total root dry weight}/\text{Total root volume};\\
\text{RSA} &= \text{Total root surface area}/\text{Vsoil};\\
\text{RV} &= \text{Total root volume}/\text{Vsoil};
\end{aligned}$$

where V_{soil} is soil core volume.

One-way analysis of variance (ANOVA) was used to test for differences in soil physicochemical parameters, and root architectural and morphological traits among the three lakes. The normality and homogeneity of the variances were tested before conducting the ANOVA. Post-hoc multiple comparisons were performed with Tukey's HSD (Honestly Significant Difference) for equal variances or Tamhane's T2 method for unequal variances (Li et al. 2018). The Spearman correlation was used to determine the main factors that significantly influence the root architectural and morphological traits. Considering the interaction between environmental factors, stepwise multiple regression analyses were conducted to further identify the key factors influencing root traits. All data analyses were performed with SPSS 13.0.

Results

Soil physicochemical parameters

The pH and MC were significantly different among the three lakes, while no significant difference was detected for OM over all seasons (Table 2). The pH was highest in Chaohu Lake and lowest in Dahuchi Lake; the MC in Chaohu Lake was significantly lower than in the other two lakes in spring, summer, and winter, but there was no significant difference between Dahuchi and Wuchang Lakes over all seasons (Table 2). The TN of Chaohu Lake was significantly lower than in Dahuchi Lake in spring and autumn, and the TP was only significantly different in spring among the three lakes (Table 2).

Architectural traits

The average values of RLD in the Chaohu, Dahuchi, and Wuchang Lakes were 3.09, 5.59, and 4.63 cm/cm^3, and the RBN was 19.55, 40.90, and 31.94 ind./cm^3, respectively. ANOVA showed that the RLD and RBN in Chaohu and Wuchang Lakes were not significantly different, although both were significantly lower than in Dahuchi Lake (RLD: $F = 7.928$, $P < 0.001$; BN: $F = 8.140$, $P < 0.001$).

Table 2 Comparison of soil characteristics in the three lakes for the four seasons using ANOVA

	Chaohu Lake (Reservoir-like type)	Dahuchi Lake (Intermittent type)	Wuchang Lake (Quasi-natural type)	*F*	*P*
Spring					
pH	8.14 ± 0.70[a]	5.81 ± 0.26[b]	7.16 ± 0.78[c]	63.317	*< 0.001*
MC (%)	19.47 ± 4.96[a]	28.05 ± 4.99[b]	25.45 ± 10.14[b]	7.233	*0.002*
OM (mg/g)	12.04 ± 8.67	16.42 ± 5.66	15.34 ± 8.65	1.587	0.214
TN (mg/g)	0.66 ± 0.41[a]	1.09 ± 0.31[b]	0.97 ± 0.47[ab]	5.648	*0.006*
TP (mg/g)	0.42 ± 0.22[ab]	0.36 ± 0.07[a]	0.53 ± 0.22[b]	3.743	*0.03*
Summer					
pH	8.00 ± 0.46[a]	6.33 ± 0.57[b]	7.19 ± 0.88[c]	32.443	*< 0.001*
MC (%)	21.40 ± 5.14[a]	27.38 ± 5.91[b]	30.73 ± 15.06[b]	4.656	*0.013*
OM (mg/g)	17.01 ± 11.28	14.96 ± 5.16	18.71 ± 20.63	0.365	0.696
TN (mg/g)	0.91 ± 0.49	1.06 ± 0.26	1.46 ± 2.03	1.072	0.349
TP (mg/g)	0.50 ± 0.67	0.37 ± 0.08	0.47 ± 0.21	0.519	0.598
Autumn					
pH	7.24 ± 0.59[a]	5.05 ± 0.32[b]	6.03 ± 0.50[c]	102.784	*< 0.001*
MC (%)	20.46 ± 7.15[a]	28.60 ± 6.25[b]	24.16 ± 7.42[ab]	6.888	*0.002*
OM (mg/g)	13.44 ± 12.10	17.82 ± 7.22	14.18 ± 9.99	1.097	0.341
TN (mg/g)	0.78 ± 0.60[a]	1.17 ± 0.38[b]	0.84 ± 0.43[ab]	3.81	*0.028*
TP (mg/g)	0.38 ± 0.31	0.39 ± 0.07	0.45 ± 0.21	0.537	0.588
Winter					
pH	7.18 ± 0.73[a]	5.09 ± 0.48[b]	6.30 ± 0.72[c]	52.862	*< 0.001*
MC (%)	16.94 ± 3.13[a]	25.10 ± 5.76[b]	25.45 ± 14.08[b]	6.367	*0.003*
OM (mg/g)	12.74 ± 7.61	15.20 ± 4.56	17.93 ± 14.03	1.417	0.252
TN (mg/g)	0.76 ± 0.46	1.07 ± 0.26	1.17 ± 0.78	3.035	0.057
TP (mg/g)	0.55 ± 0.66	0.41 ± 0.08	0.43 ± 0.11	0.658	0.522

The values are mean ± SD. Means with different lowercase superscript letters are significantly different ($P < 0.05$). Significant differences are shown in italics. *MC*, soil moisture content; *OM*, organic matter; *TN*, total nitrogen; *TP*, total phosphorus; *F*, statistical value of F test; *P*, probability value

With increases in the lakeshore elevation gradients, the RLD and RBN for plants from the three lakes also showed significant differences (Fig. 3). Both first increased and then decreased; the lowest values for both occurred at site I, and the highest values occurred at site III (Fig. 3). However, no significant differences were detected for both RLD and RBN in the three lakes over the four seasons (Fig. 4).

Morphological traits

The average values for RTD for the Chaohu, Dahuchi, and Wuchang Lakes were 0.36, 0.33, and 0.25 g/cm^3, the RSA values were 0.409, 0.799, and 0.574 cm^2/cm^3, and the RV was 0.0045, 0.0095, and 0.0059 cm^3/cm^3, respectively. ANOVA showed that the RTD in Chaohu Lake was significantly higher than in Wuchang Lake ($F = 4.198$, $P = 0.016$), while the RSA and RV in Chaohu and Wuchang Lakes were not significantly different, but they were all significantly lower than the values for Dahuchi Lake (RSA: $F = 8.732$, $P < 0.001$; RV: $F = 9.737$, $P < 0.001$). The average values of RD for Chaohu, Dahuchi, and Wuchang Lakes were 0.386, 0.424, and 0.396 mm, but there were no significant differences among the three lakes ($F = 2.163$, $P = 0.118$).

With increasing lakeshore elevation gradients, the RTD in the three lakes showed no significant differences, while the RSA and RV in the three lakes were significantly different, and both increased first and then decreased (Fig. 5). The RD in Chaohu and Dahuchi Lakes also showed significant differences along the elevation gradients, but no significant difference was found in Wuchang Lake (Fig. 5).

The variation trends for the four morphological parameters from the three lakes among the different seasons were also different (Fig. 5). The RSA and RV for plants from the three lakes were not significantly different, but the RTD was significantly different only in Wuchang Lake, and the RD was significantly different in Chaohu and Dahuchi Lakes (Fig. 6).

Influencing factors

Spearman correlation analyses showed that the duration, depth, amplitude, and pH were significantly correlated with the two architectural parameters (RLD and RBN),

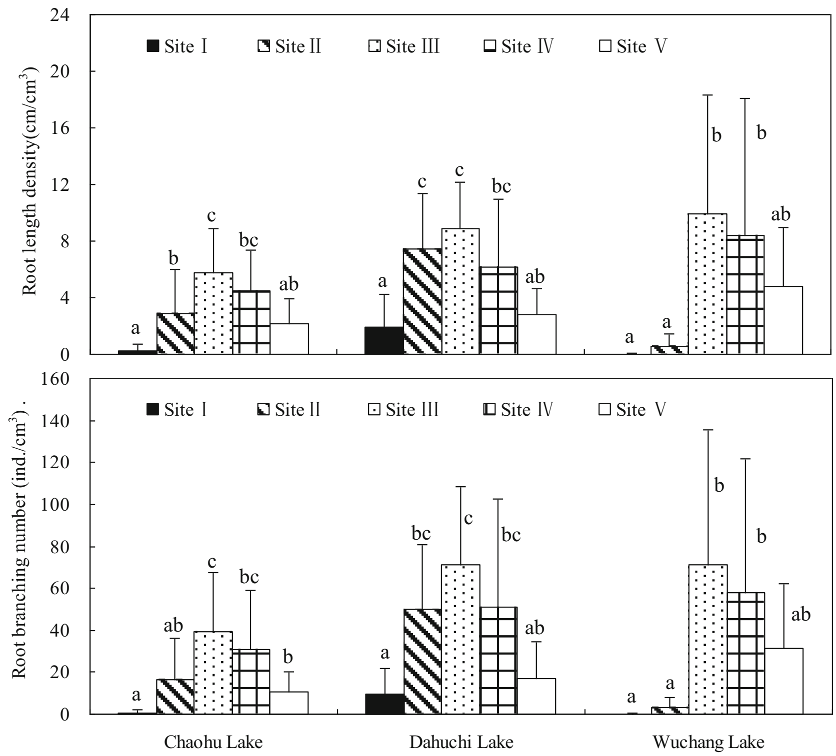

Fig. 3 Comparisons of root length density (RLD) and root branching number (RBN) in the three lakes along the lakeshore elevation gradients (sites I–V). Values with different lowercase superscript letters are significantly different at $P < 0.05$, ns denotes no significance. Values are mean ± standard deviation (SD)

and the OM only showed significant effects on RBN (Table 3). The duration, depth, OM, and pH were strongly correlated with the four morphological parameters (RTD, RSA, RV, and RD), and the effects of MC, TP, TN, and amplitude were only significant for certain morphological parameters (Table 3). From the correlation coefficients (R) given in Table 3, we can readily see that the most prominent correlations are between duration and almost all root

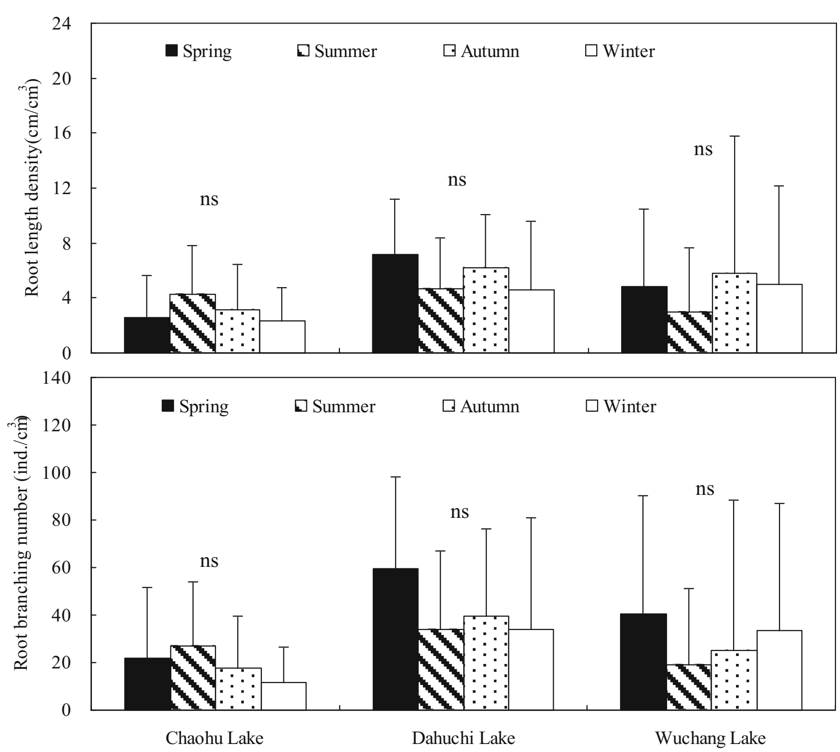

Fig. 4 Comparisons of root length density (RLD) and root branching number (RBN) for the three lakes in the four seasons of the year. Values with different lowercase superscript letters are significantly different at $P < 0.05$, ns denotes no significance. Values are mean ± SD

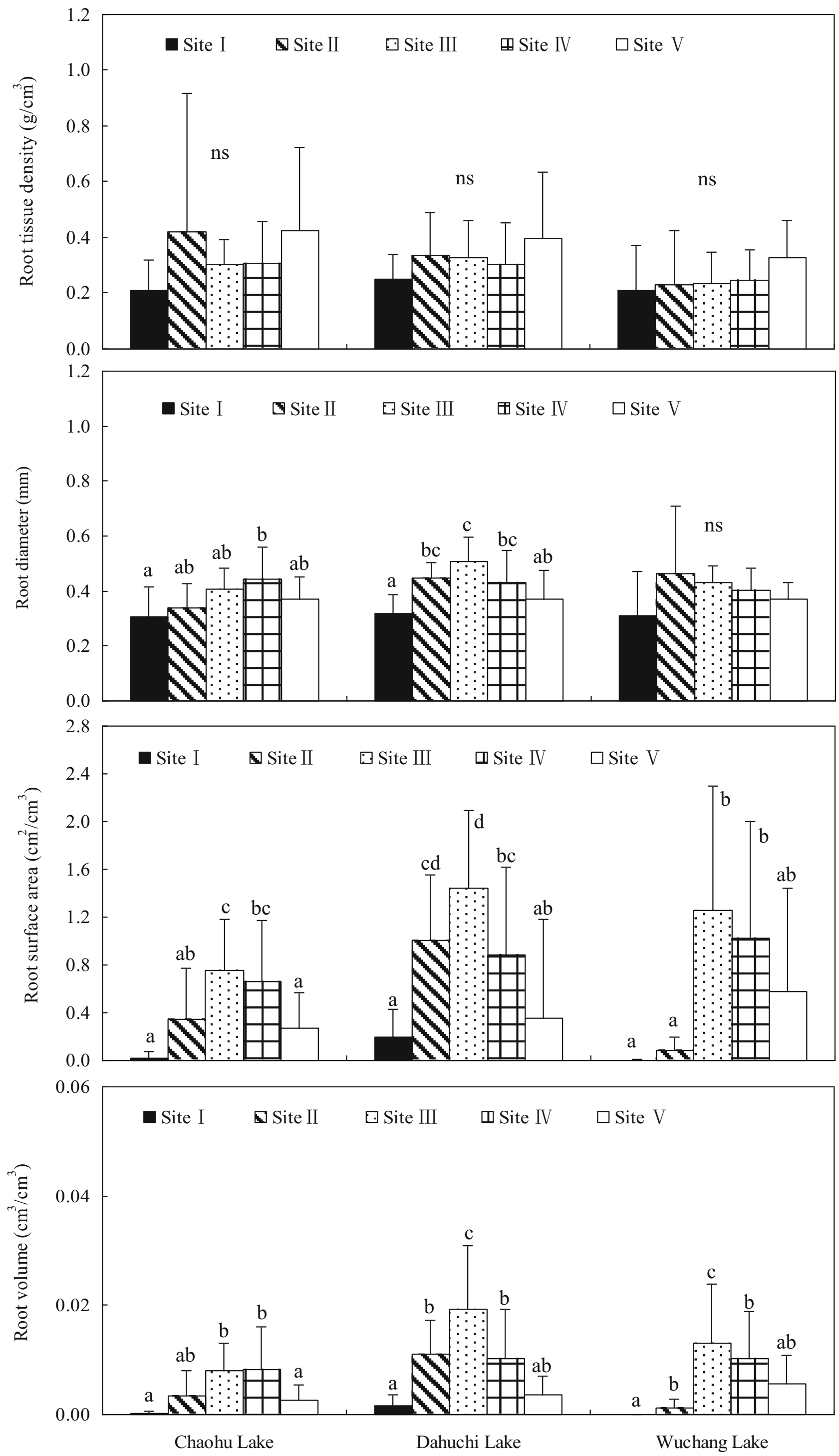

Fig. 5 Comparisons of root morphological parameters for the three lakes along the lakeshore elevation gradients. Values with different lowercase superscript letters are significantly different at $P < 0.05$, ns denotes no significance. Values are mean ± SD

traits, so statistically, the most important factor influencing the root traits should be duration.

The results of stepwise multiple regression show that duration is the first factor that enters the regression equation, followed by pH in most cases when root traits were selected as the y variables (Table 4). This further indicates that duration is the key factor that influences root traits.

Discussion

Soil physicochemical parameters

Many studies have shown that WLFs have important effects on lakeshore soil environments (Furey et al. 2004; Leira and Cantonati 2008; Ding 2013). In the case of submergence, the

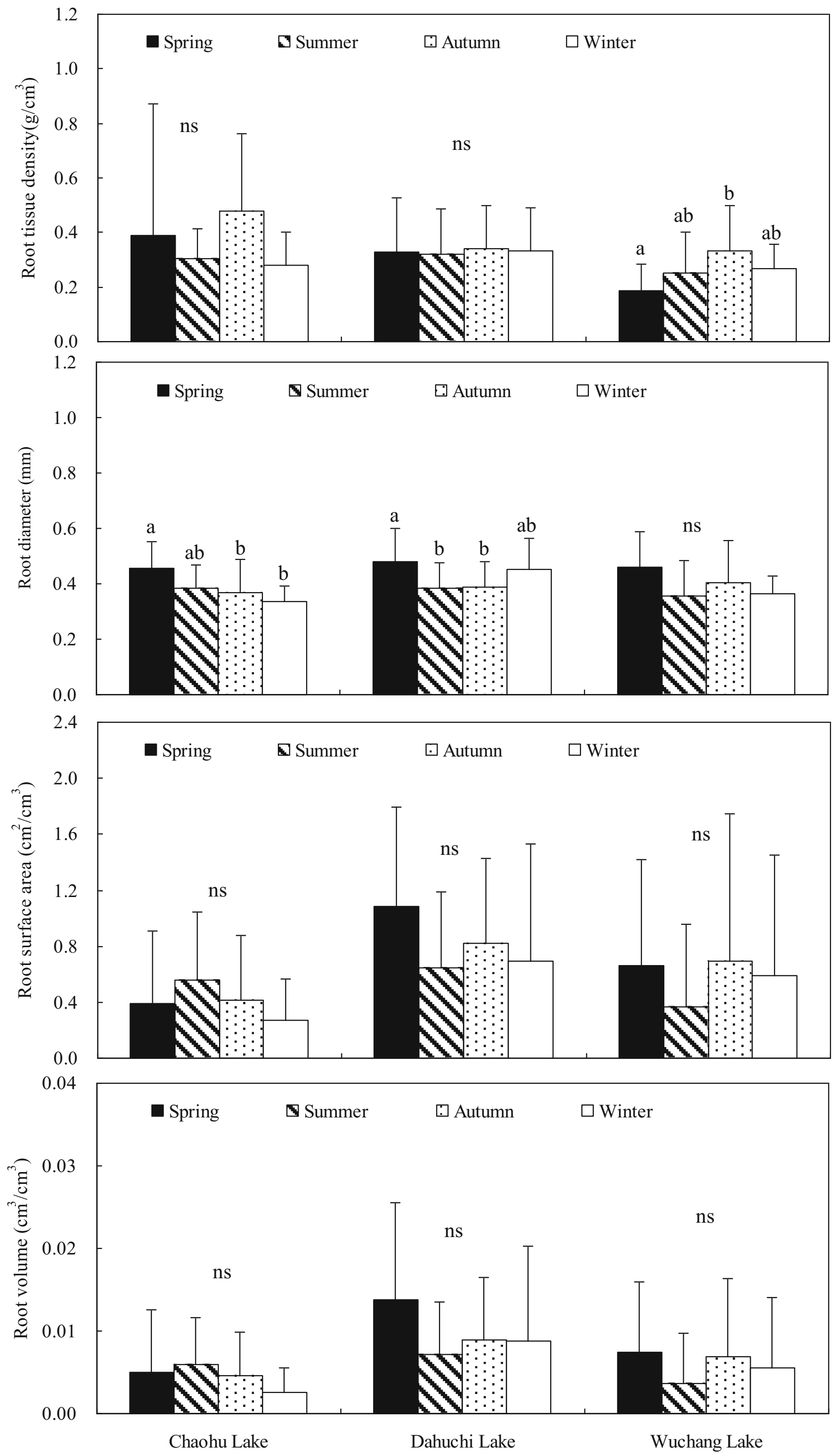

Fig. 6 Comparisons of root morphological parameters for the three lakes over the four seasons of the year. Values with different lowercase superscript letters are significantly different at $P < 0.05$, ns denotes no significance. Values are mean ± SD

oxygen content of the soil will decrease, and a variety of reducing gases are produced by anaerobic microorganisms, which leads to a decrease in the soil oxidation-reduction potential and an increase in pH (Narteh and Sahrawat 1999; Ding 2013). In this study, the pH was the highest in Chaohu Lake and the lowest in Dahuchi Lake. This may be mainly because the WLFs in Chaohu Lake are reservoir-like, and the lakeshore is submerged for a long time due to the increased annual mean water level, while the lakeshore of Dahuchi Lake is only submerged during the brief high water level period. There were also significant differences in soil MC for the three lakes, and it was the lowest in Chaohu Lake in all seasons of the year. This could be due to the fact that the substrate around the lakeshore of Chaohu Lake is mainly composed of sand,

Table 3 Spearman correlation coefficients (*R*) between root morphological and architectural traits and environmental parameters. Significant correlations are shown in italics

	Root length density	Root branching number	Root tissue density	Root diameter	Root surface area	Root volume	pH	MC	OM	TN	TP	Amplitude	Depth	Duration	Frequency
Root length density	1.00	*0.98*	*0.93*	*0.57*	*0.99*	*0.97*	*− 0.28*	0.16	0.31	0.24	− 0.13	*0.27*	*− 0.41*	*− 0.41*	− 0.01
Root branching number		1.00	*0.91*	*0.59*	*0.98*	*0.97*	*− 0.31*	0.21	*0.23*	0.25	− 0.11	*0.31*	*− 0.41*	*− 0.39*	− 0.03
Root tissue density			1.00	*0.64*	*0.94*	*0.94*	*− 0.30*	0.10	*0.31*	0.24	*− 0.26*	*0.29*	*− 0.50*	*− 0.51*	0.00
Root diameter				1.00	*0.64*	*0.70*	*− 0.30*	*0.35*	*0.55*	*0.48*	− 0.10	0.25	*− 0.28*	*− 0.39*	− 0.21
Root surface area					1.00	*0.99*	*− 0.28*	0.17	*0.34*	*0.27*	− 0.15	*0.27*	*− 0.43*	*− 0.44*	− 0.02
Root volume						1.00	*− 0.29*	0.20	*0.37*	*0.29*	− 0.16	*0.27*	*− 0.43*	*− 0.45*	− 0.02
pH							1.00	*− 0.72*	*− 0.36*	*− 0.53*	− 0.07	*− 0.89*	− 0.01	0.00	*0.33*
MC								1.00	*0.59*	*0.68*	*0.28*	*0.55*	*0.31*	0.24	*− 0.27*
OM									1.00	*0.93*	*0.38*	0.17	− 0.11	*− 0.32*	*− 0.28*
TN										1.00	*0.47*	*0.37*	− 0.09	*− 0.31*	*− 0.35*
TP											1.00	0.16	0.05	− 0.01	− 0.16
Amplitude												1.00	− 0.09	− 0.08	− 0.24
Depth													1.00	*0.89*	− 0.09
Duration														1.00	0.00
Frequency															1.00

MC, soil moisture content; *OM*, organic matter; *TN*, total nitrogen; *TP*, total phosphorus; *amplitude*, amplitude of WLFs; *depth*, mean submergence depth; *duration*, duration of submergence; *frequency*, frequency of submergence

Table 4 Stepwise multiple regression analyses between significant environmental parameters and morphological and architectural root traits

	N	*F*	*R*	*P*	Key factor 1 (X1)	Key factor 2 (X2)	Key factor3 (X3)
Architectural traits							
Root length density	60	8.229	0.352	0.006	Duration	–	–
Root branching number	60	5.14	0.391	0.009	Duration	pH	–
Morphological traits							
Root tissue density	60	7.435	0.534	< 0.001	Duration	pH	TP
Root surface area	60	7.847	0.465	0.001	Duration	pH	–
Root volume	60	8.836	0.486	< 0.001	Duration	pH	–
oot diameter	60	12.734	0.559	< 0.001	Duration	MC	–

MC, soil moisture content; *TP*, total phosphorus; *duration*, duration of submergence; *N*, sample size; *F*, statistical value of F test; *R*, goodness of fit index; *P*, probability value

and it does not hold water well. According to a study of the Yangtze floodplain lakes, the proportion of sand in the Chaohu Lake soil is 86.2%, while in Dahuchi Lake it is only 16.4% (Ding 2013). Otherwise, although there was no significant difference in the OM in the three lakes, OM was also the lowest in Chaohu Lake in all seasons. This may be due to the low level of vegetation coverage in the lakeshore area of Chaohu Lake, which reduces the source of organic matter; similar results have been reported for the riparian zone of Three Gorges Dam (Chang et al. 2011). Some studies have also shown that WLFs have important effects on TN and TP; raising the water level can lead to declines in the levels of TN and TP in the soil, and long-term high water levels are not conducive to the accumulation of TN and TP (Qiu and McComb 1996; Ding 2013). TN was the lowest in Chaohu Lake in different seasons, and this may be mainly related to the long duration of high water levels. However, the TP did not show a similar trend in this study, and the reasons for this need to be further analyzed.

Architectural and morphological traits

The architectural and morphological traits of roots have important implications for many ecosystem processes (Bardgett et al. 2014); thus, the study of root traits will help us understand the ecological roles of plant roots in aquatic ecosystems. The RLD and RBN mainly reflect the spatial configuration of the roots (Bardgett et al. 2014). The present study shows that the RLD and RBN in the three lakes are significantly different, and that the spatial configuration was the most complex in Dahuchi Lake and the simplest in the Chaohu Lake. The different vegetation types produced by different WLFs in the three lakes may be the main cause (Zhang 2013; Zhang et al. 2015). The lakeshore area of Chaohu Lake is mainly covered by *Cynodon dactylon*, and the shore of Dahuchi Lake is mainly dominated by *Carex* (Zhang et al. 2015). Although both species possess fibrous root systems, the root distribution of *C. dactylon* is mainly concentrated in the surface 0–10 cm soil (Xu and Zeng 2008), while *Carex* roots are mainly distributed in the 0–20 cm soil layer (Deng et al. 2016), with a maximum distribution depth of ~ 50 cm (Kang et al. 2016). This indirectly indicates that the ability of plant roots to strengthen dykes and remove nutrients from the lakeshore may be the poorest in lakes with reservoir-like WLFs. With increases in the elevation gradient, the RLD and RBN in all three lakes showed significant differences, and both parameters reached their maxima at site III, which supports the intermediate disturbance hypothesis. However, no significant differences were found when it comes to the different seasons. This may be because the three lakes were mainly dominated by perennial hygrophytes in the lakeshore areas, and the roots have developed corresponding strategies (such as dormancy) to tolerate submergence or other less-than-ideal conditions.

The RSA and RV in Dahuchi Lake were also significantly higher than in the other two lakes, and the variation trends for the two morphological parameters along the elevation gradients or in the different seasons were the same as for the RLD and RBN. This can be explained by the strong correlations (correlation coefficient $R > 0.9$) between the two architectural parameters and the two morphological parameters (Table 3). RTD is a fundamental trait in comparative root ecology, and is often used as an indicator of plant strategies (Birouste et al. 2011). Plants with low RTD show a relatively fast growth rate and rapid resource acquisition (Wahl and Ryser 2000; Hummel et al. 2007), but usually have a shorter life span compared with high-RTD species (Tjoelker et al. 2005). The lowest RTD in Wuchang Lake may be because the WLFs are of the quasi-natural type, which provides relatively favorable conditions for root growth. The RD is also an important trait that reflects the status of roots, but the findings related to RD are usually different. For example, the RD of some *Rumex* species was larger in frequently waterlogged soil than in rarely flooded soil in order to facilitate the diffusion of gases to the root tip (Visser et al. 1996); however, the RD of *Deyeuxia angustifolia* decreased with increasing water levels due to the limited oxygen and reduced soil redox potential (Xie et al. 2008). In our study, the changes in RD along the elevation gradient or in the different seasons in the three lakes were not uniform, indicating that the morphological responses of RD to WLFs may vary.

Influencing factors

In addition to frequency, both the physicochemical parameters and other hydrological parameters had significant effects on the architectural or morphological root traits examined in this study. This was mainly because the frequency is low in lakes compared with rivers, and similar results related to the impacts of frequency on plant distribution have been reported by Zhang et al. (2014). Among the several environmental parameters that determine root traits, the duration is the most important factor, followed by depth and pH based on the correlation coefficients (*R*). However, due to the significant interactions among environmental factors, duration was the first entered factor when the stepwise multiple regression was made, followed by the pH. Duration is usually recognized as the main factor influencing the community structure of vegetation (Ye et al. 2013; Zhang et al. 2015). With increases in duration, the dominant species will shift from flood-sensitive to flood-tolerant species (Lenssen and De Kroon 2005), and the root traits will inevitably also change considerably. The pH is also an important factor determining the growth of plant roots, because it is closely related to the oxidation-reduction potential of the soil (Narteh and Sahrawat 1999). According to Ding (2013), plant roots live best in acidic soils with pH of 5–6 in lakeshore areas of the Yangze River floodplain lakes. Therefore, the suitable pH in the Dahuchi Lake lakeshore soil over all four seasons provided better conditions for the development of plant roots compared with the other two lakes.

Implications for lake management and further studies

In view of their importance in ecosystems, studies of plant roots are garnering increasing attention (Bardgett et al. 2014). However, most of the current studies have been conducted using simulation experiments (e.g., Zobel et al. 2007; Xie et al. 2008; Wang et al. 2016). Among the few field studies, most are focused on desert plants (Yang et al. 2008; Shan et al. 2013) or grassland species (Luo et al. 2011). The present study represents the first quantitative research on root traits in lakeshore areas of floodplain lakes, and the results have important implications for the management of lakes and reservoirs. Our study showed that WLFs have significant effects on the architectural and morphological root traits, and also showed that the root spatial configuration was the simplest in lakes with reservoir-like WLFs. This is consistent with the results from studies of the aboveground parts of lakeshore plants showing that plant diversity and coverage are low in lakes with reservoir-like WLFs (Zhang 2013). Because the spatial configuration of roots is closely related to the stability of the soil (Xu and Zeng 2008), it is necessary to adjust the WLF model in reservoir-like lakes. Otherwise, Poyang Lake, as one of the remaining three river-connected lakes, will be blocked by a dam in the foreseeable future, which will directly lead to an alteration of the water regime in the lakes with intermittent WLFs around Poyang Lake. Because root spatial configuration was the most complex in this type of lake, changes in root traits may have disadvantageous effects on the ecological functions of Poyang Lake.

In this study, the measurement of root traits is difficult and time consuming mainly due to the small diameter, irregular shape, and complex configuration of the roots. Therefore, only four transects were set on the lakeshore of each lake. Knowing that the roots of most plants are concentrated in the top 20 cm soil, we used a sampling depth in this study of 17 cm. In future studies, it will be necessary to consider the following two points: first, quantitatively analyze the changes in root traits in different soil layers in the lakeshore area. The sampling depth should be increased, and the plant roots in different soil layers should be collected separately when conducting field investigations. Second, in order to better predict the changes in root traits, the lakeshore plants should be classified into different water level-limited guilds.

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References

Bardgett RD, Mommer L, De Vries FT (2014) Going underground: root traits as drivers of ecosystem processes. Trends Ecol Evol 29(12): 692–699

Birouste M, Kazakou E, Blanchard A, Roumet C (2011) Plant traits and decomposition: are the relationships for roots comparable to those for leaves? Ann Bot 109(2):463–472

Chang C, Xie ZQ, Xiong GM, Chu LM (2011) The effect of flooding on soil physical and chemical properties of riparian zone in the Three Gorges Reservoir. J Nat Resour 26(7):1236–1244 (in Chinese)

Chapman N, Miller AJ, Lindsey K, Whalley WR (2012) Roots, water, and nutrient acquisition: let's get physical. Trends Ecol Evol 17: 701–710

Coops H, Beklioglu M, Crisman TL (2003) The role of water–level fluctuations in shallow lake ecosystems–workshop conclusions. Hydrobiologia 506(509):23–27

Deng ZM, Zhang X, Zhang H, Pan GY, Qin XQ (2016) Analysis of stable oxygen isotope of soil-plant-groundwater in Poyang Lake wetland. Resour Environ Yangtze Basin 25(6):989–995 (in Chinese)

Ding QZ (2013) Impacts of water level fluctuations on substrate environments of lakeshore vegetation. Dissertation of University of Chinese Academy of Sciences (in Chinese)

Furey PC, Nordin RN, Mazumder A (2004) Water level drawdown affects physical and biogeochemical properties of littoral sediments of a reservoir and a natural lake. Lake Reserv Manage 20(4):280–295

Hummel I, Vile D, Violle C, Devaux J, Ricci B, Blanchard A, Garnier E, Roumet C (2007) Relating root structure and anatomy to whole-plant functioning in 14 herbaceous Mediterranean species. New Phytol 173(2):313–321

Kang JJ, Zhao M, Li GY, Zhang JQ, Wang F (2016) Preliminary study on the sand-fixing characteristics of Carex brunnescens in desertification grassland of Maqu County. Soil Water Conser China 2:47–51 (in Chinese)

Lambers H, Raven JA, Shaver GR, Smith SE (2008) Plant nutrient-acquisition strategies change with soil age. Trends Ecol Evol 23(2):95–103

Leira M, Cantonati M (2008) Effects of water-level fluctuations on lakes: an annotated bibliography. Hydrobiologia 613:171–184

Lenssen JPM, De Kroon H (2005) Abiotic constraints at the upper boundaries of two Rumex species on a freshwater flooding gradient. J Ecol 93(1):138–147

Li ZF, Zhang XK, Wan A, Wang HL, Xie J (2018) Effects of water depth and substrate type on rhizome bud sprouting and growth in *Zizania latifolia*. Wetl Ecol Manag 26(3):277–284

Lu RS (2000) Soil and agriculture chemical analysis methods. Chinese agricultural science and technology press, Beijing (In Chinese)

Luo WT, Wu YN, Zhang FJ, Huo GW, Lv JZ (2011) Root characteristics under different grazing intensities in *Stipa krylovii steppe*. Chin J Ecol 30(12):2692–2699 (In Chinese)

Lytle DA, Poff NL (2004) Adaptation to natural flow regimes. Trends Ecol Evol 19:94–100

Magee TK, Kentula ME (2005) Response of wetland plant species to hydrologic conditions. Wetl Ecol Manag 13(2):163–181

Narteh LT, Sahrawat KL (1999) Influence of flooding on electrochemical and chemical properties of West African soils. Geoderma 87(3):179–207

Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytol 193(1):30–50

Qiu S, McComb AJ (1996) Drying-induced stimulation of ammonium release and nitrification in reflooded lake sediment. Mar Freshw Res 47(3):531–536

Shan LS, Li Y, Ren W, Su SP, Dong QL, Geng DM (2013) Root architecture of two desert plants in central Hexi corridor of Northwest China. Chin J Appl Ecol 24(1):25–31 (in Chinese)

Tjoelker MG, Craine JM, Wedin D, Reich PB, Tilman D (2005) Linking leaf and root trait syndromes among 39 grassland and savannah species. New Phytol 167(2):493–508

Visser EJ, Blom CW, Voesenek LA (1996) Flooding-induced adventitious rooting in *Rumex*: morphology and development in an ecological perspective. Acta Botanica Neerlandica 45(1):17–28

Wahl S, Ryser P (2000) Root tissue structure is linked to ecological strategies of grasses. New Phytol 148(3):459–471

Wang SM, Dou HS (1998) Lakes of China. Science Press, Beijing (In Chinese)

Wang P, Deng X, Huang Y, Fang X, Zhang J, Wan H, Yang C (2016) Root morphological responses of five soybean [*Glycine max* (L.) Merr] cultivars to cadmium stress at young seedlings. Environ Sci Pollut Res 23:1860–1872

Wantzen KM, Rothhaupt KO, Mörtl M, Cantonati M, László G, Fischer P (2008) Ecological effects of water-level fluctuations in lakes: an urgent issue. Hydrobiologia 613(1):1–4

Xie Y, Luo W, Wang K, Ren B (2008) Root growth dynamics of Deyeuxia angustifolia seedlings in response to water level. Aquat Bot 89(3):292–296

Xu SJ, Zeng B (2008) Enhancement effects of 5 flooding-tolerant species' roots on soil anti-erodibility in Three Gorges reservoir region. J Soil Water Conserv 22(6):13–18 (In Chinese)

Yang XL, Zhang XM, Li YL, Li SC, Sun HL (2008) Analysis of root architecture and root adaptive strategy in the Taklimakan Desert area of China. Chin J Plant Ecol 32:1268–1276 (In Chinese)

Ye C, Zhang K, Deng Q, Zhang Q (2013) Plant communities in relation to flooding and soil characteristics in the water level fluctuation zone of the three gorges reservoir, China. Environ Sci Pollut Res 20(3):1794–1802

Yuan S, Yang Z, Liu X, Wang H (2017) Key parameters of water level fluctuations determining the distribution of Carex in shallow lakes. Wetlands 37:1005–1014. https://doi.org/10.1007/s13157-017-0934-0

Zhang XK (2013) Water level fluctuation requirements of plants in the Yangtze floodplain lakes. Dissertation of University of Chinese Academy of Sciences (In Chinese)

Zhang X, Liu X, Wang H (2014) Developing water level regulation strategies for macrophytes restoration of a large river–disconnected lake, China. Ecol Eng 68:25–31

Zhang X, Liu X, Wang H (2015) Effects of water level fluctuations on lakeshore vegetation of three subtropical floodplain lakes, China. Hydrobiologia 747:43–52

Zhang X, Wan A, Wang H, Zhu L, Yin J, Liu Z, Yu D (2016) The overgrowth of Zizania latifolia in a subtropical floodplain lake: changes in its distribution and possible water level control measures. Ecol Eng 89:114–120

Zobel RW, Kinraide TB, Baligar VC (2007) Fine root diameters can change in response to changes in nutrient concentrations. Plant Soil 297(1–2):243–254