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Interactive influence of water level, sediment heterogeneity, and plant density on the growth performance and root characteristics of *Carex brevicuspis*

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ABSTRACT

Water level, sediment heterogeneity, and plant density are important factors that determine plant growth, distribution, and community structure. In the present study, we investigated the effects of these factors on the growth and root characteristics of *Carex brevicuspis*. We conducted an outdoor experiment to monitor biomass accumulation and allocation, relative root distribution mass ratio, longest root length, and total N and P contents of *C. brevicuspis* plants. We used a factorial design with two water levels (0 cm and −15 cm relative to the soil surface, named high and low water level treatments, respectively), three sediment types (sand/clay sediment with 0–15 cm of sand and 15–30 cm of clay; mixed sediment with 0–30 cm mixture of sand and clay with 1:1 volumw ratio; and clay/sand sediment with 0–15 cm of clay and 15–30 cm of sand), and three plant densities (88 plants per m^2, 354 plants per m^2, and 708 plants per m^2). Biomass accumulation decreased with increasing plant density and was significantly higher in the low water level and the clay/sand sediment than in the high water level and the other two sediment types. The shoot:root ratio was markedly higher in the high water level than in the low water level and decreased with increasing plant density; further, in the high water level, it was significantly lower in the sand/clay sediment than in the other two sediment types. The relative root distribution mass ratio was markedly higher in the high water level treatments than in the low water level treatments. Further, in the high water level treatments, the relative root distribution mass ratio increased with increasing plant density in the clay/sand sediment and was lower in the sand/clay sediment than in the other two sediment types. The longest root length was significantly lower in the high water level than in the low water level and increased with increasing plant density in the sand/clay sediment in the high water level. Total N content in the plants was influenced only by sediment type; on the other hand, total P content was markedly higher in the high water level than in the low water level. Our data indicate that growth of *C. brevicuspis* was limited by higher water level, higher density and sand/clay sediment. Plants can increase shoot:root ratio and develop shallow root system to acclimate to high water level and thus could adjust shoot:root ratio and root characteristics, e.g. decrease their shoot:root ratio and allocating more root and increasing root length to the nutrient rich layer to acclimate to conditions of higher density and sediment heterogeneity.

1. Introduction

Flooding is the main factor that determines plant growth and distribution in wetland ecosystems, mainly because of the reduced oxygen availability and decreased redox potential of flooded soil (Blom and Voesenek, 1996; Deegan et al., 2007). In general, a long period of acclimation enables wetland plants to tolerate a certain degree of flooding stress via morphological (e.g., biomass allocation, aerenchyma, and root system) and physiological (e.g., malondialdehyde and proline) adjustments (Blom and Voesenek, 1996; Luo and Xie, 2009; Li et al., 2013). However, in some wetlands (e.g., river-connected lakes and floodplains), water-deficit events occur frequently and have an influence on plant growth

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(Pagter et al., 2005; Parolin et al., 2010; Li et al., 2013). The acclimation of wetland plants to flooding has been extensively studied (Deegan et al., 2007; Luo and Xie, 2009); however, data regarding the acclimation of these plants to water-deficit conditions are lacking.

Besides water availability, wetland plants are exposed to many other environmental stressors such as sedimentation, nutrient limitation, and nutrient heterogeneity (Frank and Peterson, 2003; Xie et al., 2007; Luo and Xie, 2009); moreover, the effects of these factors may interact with those of water availability. For example, in *Deyeuxia angustifolia*, increases in root diameter caused by enhanced nutrient supply can increase oxygen transport to the root tips and facilitate acclimation to high water levels (Xie et al., 2009). Several studies have investigated the interactive effects of water level and nutrient availability on plant performance (Wetzel and van der Valk, 1998; Xie et al., 2009). Owing to complex hydrological processes, sediment stratification is observed more frequently in natural aquatic habitats than in terrestrial systems (Klump and Martens, 1989; Xie et al., 2007) and may affect plant growth performance and root architectures. For example, when the top soil layer is nutrient limited, *Vallisneria natans* increases its root mass fraction and enhances the root length to the bottom soil layer, to obtain sufficient nutrients (Xie et al., 2007). To date, however, few studies have investigated the effects of nutrient heterogeneity—particularly nutrient stratification—on plant growth performance.

Besides abiotic environmental factors, biotic factors such as plant density are important determinants of plant growth and reproduction (Shilo-Volin et al., 2005; Li et al., 2009). Under conditions of low plant density, intraspecific facilitation may be important, whereas under a dense canopy, plant growth may be limited by strong intraspecific competition (Li et al., 2009, 2014). Optimal partitioning models suggest that plants respond to environmental variation by partitioning biomass between different plant organs, to optimize the capture of nutrients, light, water, and carbon dioxide in a manner that maximizes plant growth (Dou et al., 2010). Plastic responses to high plant density not only include the reallocation of resources between shoots and roots, but also include a shift from sexual to vegetative reproduction and adjustment of root system, e.g. development of deep root systems in homogeneous sediment and allocation of more root to nutrient rich sediment layer in heterogeneous sediment (Li et al., 2014). These changes not only increase the plant's acquirement of resources, but also influence its responses to other environmental factors. Previous studies have shown that increases in plant density stimulate responses to flooding (Luo et al., 2010), wind (Retuerto et al., 1996), and burial stress (Li et al., 2014). However, the interactive effects of plant density, water level, and nutrient heterogeneity on plant growth performance remain unclear.

In the present study, we investigated the interactive effects of water level, plant density, and sediment heterogeneity on the growth performance and root characteristics of *Carex brevicuspis*—a dominant wetland plant in the Dongting Lake Wetland, China. In this lake, wetland plants are generally distributed along a water level gradient (e.g., high water level species such as *Miscanthus sacchariflorus*, medium water level species such as *C. brevicuspis* and *Polygonum hydropiper*, and low water level species such as *Phalaris arundinacea*). We used a factorial design with two water levels (0 cm and −15 cm relative to the soil surface, named high water level and low water level, respectively), three sediment types (sand/clay sediment with 0–15 cm of sand and 15–30 cm of clay; mixed sediment with 0–30 cm mixture of sand and clay with 1:1 volume ratio; and clay/sand sediment with 0–15 cm of clay and 15–30 cm of sand), and three densities (low, 88 plants per m^2; medium, 354 plants per m^2; and high, 708 plants per m^2). We monitored biomass accumulation and allocation, relative root distribution mass ratio, longest root length, and total N and P contents. We predicted that (1) biomass accumulation and total N and P contents decrease with increasing plant density and would be significantly higher in the higher water level and the clay/sand sediment than in the low water level and the other two sediment types because of intraspecific competition in the higher density treatment, better water condition and nutrient availability in the high water level and clay/sand sediment, respectively; (2) the shoot:root ratio and the relative root distribution mass ratio decrease with increasing plant density and would be significantly higher in the high water level and the clay/sand sediment than in the low water level and the other two sediment types, which would benefit the plants to acclimate to intensified intraspecific competition, water deficit and lower nutrient availability conditions; (3) the longest root length increases with increasing plant density and would be significantly lower in the high water level and the clay/sand sediment than in the low water level and the other two sediment types, which would benefit the plants in acclimating to intensified intraspecific competition, water deficit and lower nutrient availability conditions.

2. Materials and methods

2.1. Study area

Dongting Lake (111°40′–113°10′E, 28°30′–30°20′N) is the second largest freshwater lake and the most typical river-connected lake in China. The Dongting wetlands are characterized by large seasonal fluctuations in water levels; these wetlands are completely flooded from May to October and are subject to drought conditions from November to April.

2.2. Plant materials

We chose *Carex brevicuspis* (Cyperaceae) as the target plant because it is a typical perennial rhizomatous species that is widely distributed in eastern mainland China and Taiwan (Dai et al., 2010). In Dongting Lake, this species forms a monodominant community or co-dominates with other *Carex* species or *M. sacchariflorus*, and it usually flowers and fruits from April to May, before flooding occurs (Chen et al., 2011). During the flood season, the vegetation is completely submerged and the aboveground shoots senesce. After flooding, *C. brevicuspis* shoots emerge immediately (November) and grow into vegetative ramets by January. In January, plants remain relatively dominant, but the shoots partially wither because of low temperature. New ramets sprout in February or March and grow rapidly (Deng et al., 2013). This species distributes widely along an elevation gradient with various of sediment types in the Dongting Lake.

In the present study, plants were collected during February 2014 in Junshan County, East Dongting Lake (112°59′40.0″E, 29°22′17.7″N), after the sprouting of new ramets. The vegetation was cut into small blocks (20 cm × 20 cm) and transported to an experimental field at the Dongting Lake Station for Wetland Ecosystem Research, which is run by The Chinese Academy of Sciences. Plant fragments (with roots) were placed in plastic buckets containing 15 cm of soil (collected from a *C. brevicuspis* community; 1.45% organic matter, 4.04 $\mu g\, g^{-1}$ of exchangeable N, and 0.88 $\mu g\, g^{-1}$ of exchangeable P) to germinate new ramets. The plants were watered when necessary.

2.3. Experimental design

The experiment combined two water levels (0 cm and −15 cm relative to the soil surface, named high water level and low water level, respectively), three plant densities (88 plants per m^2, 354

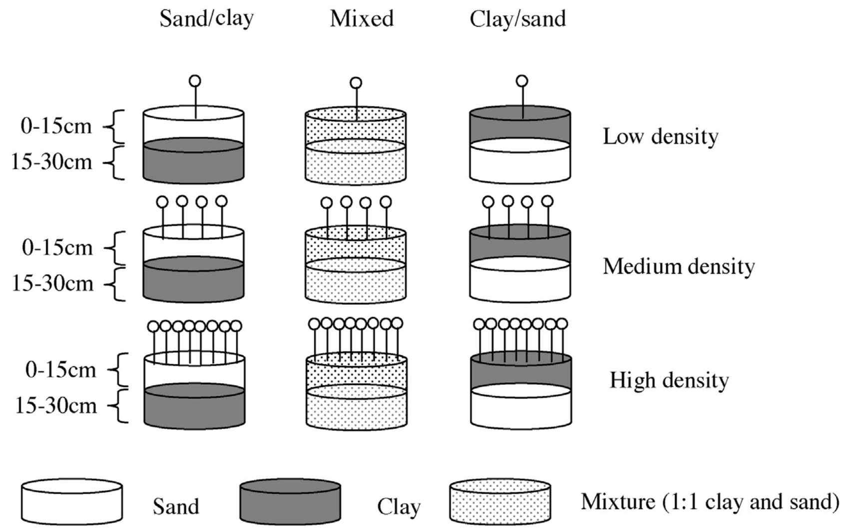

Fig. 1. Experimental scheme, showing the three sediment types (sand/clay; mixed; clay/sand) and three plant densities. Each treatment was conducted at 0-cm and 15-cm water levels, with five replications.

plants per m^2, and 708 plants per m^2), and three sediment types (sand/clay sediment with 0–15 cm of sand and 15–30 cm of clay; mixed sediment with 0–30 cm mixture of sand and clay with 1:1 volume ratio; and clay/sand sediment with 0–15 cm of clay and 15–30 cm of sand) in a factorial design with five replicates. The depth of the sediment was based on the investigation of root length of *C. brevicuspis*. The 18 treatments—nine 0-cm water level treatments and nine −15-cm water level treatments—are summarized in Fig. 1. The plant densities were selected based on results of a six-year field investigation of *C. brevicuspis* community in the Dongting Lake (density ranging from 400 to 1600 plants per m^2).

We cut 390 ramets of similar size (3–4 leaves, approximately 25 cm in height) from the plant cultures on March 22, 2014. We planted these ramets in PVC tubes (30 cm in height and 12 cm in diameter) filled with sediment. Nine tubes (one tube per sediment type and plant density treatment) were placed into each of 10 large plastic bins (98 cm × 76 cm × 68 cm) to control the water level (five bins per water level). The plastic bins were placed in an outdoor area with natural illumination at the Dongting Lake Station. The experiment commenced seven days after planting. We used two water levels—0 cm relative to the soil surface (control) and −15 cm relative to the soil surface (water-deficit treatment). We used tap water containing 0.511 $\mu g L^{-1}$ of NH_4^+-N, 1.760 $\mu g L^{-1}$ of NO_3^--N, and 0.527 $\mu g L^{-1}$ of PO_4^{3+}-P, pH = 7.2). We controlled the water level by drilling two holes at the required height to drain surplus water after rain. We replenished the water daily and replaced the water once a week to prevent algal growth. Clay was collected from the same location as that used for ramet germination. Sand was collected from a local river (Xiang River) and contained 0.76 $g kg^{-1}$ of organic matter, 0.25 $g kg^{-1}$ of exchangeable N, and 0.06 $g kg^{-1}$ of exchangeable P.

2.4. Harvesting and root characteristics

The plants were harvested after three months, following the growth cycle of *C. brevicuspis*. The roots were carefully dug out by hand and washed under tap water. The longest root length was measured with a 0.1-cm unit ruler, and the plants were then divided into the above-ground part and the 0–15-cm and 15–30-cm belowground parts, oven-dried at 80 °C for 48 h, and weighed. The rhizome of *C. brevicuspis* contains a small amount of biomass; hence, we did not separate the leaf and the rhizome in this study. Plant biomass was calculated as the total dry mass of all the plant tissues. The shoot:root ratio was determined as the ratio of the above-ground mass to the below-ground mass (sum of the 0–15-cm and 15–30-cm belowground masses). The relative root distribution mass ratio was defined as the ratio of the 0–15-cm belowground mass to the 15–30-cm belowground mass.

2.5. Total N and P contents

After collection, the plant above-ground parts were ground into a powder and mixed. The samples were digested with a mixture of H_2SO_4 and H_2O_2, and the N and P concentrations were measured using colorimetric analysis with a TU-1901 spectrophotometer (Shi, 1994). Three replicates of each sample were included (Xie et al., 2007).

2.6. Statistical analysis

We conducted three-way analysis of variance with water level, sediment type, and plant density as the main factors, and biomass accumulation, biomass allocation, relative root distribution mass ratio, the longest root length, total N content, and total P content as the response variables. Means were compared using Duncan's test at the 0.05 significance level. Where necessary, data were $\log_{10}$-transformed to reduce the heterogeneity of variances. Normality and homogeneity were tested using Lilliefors and Levene's tests, respectively. All the analyses were performed using SPSS 15.0 for Windows.

3. Results

3.1. Biomass accumulation

Biomass accumulation significantly decreased with increasing plant density (Table 1; Fig. 2A and B). In addition, it was significantly higher in the low water level and the clay/sand sediment than in the high water level and the other two sediment types. The highest biomass accumulation was 16.16 ± 1.02 g, which occurred in the low water level + low plant density + clay/sand sediment treatment (Fig. 2A and B). This value was 8.55-fold higher than the lowest biomass accumulation (1.89 ± 0.18 g), which occurred in the high water level + high plant density + sand/clay sediment treatment (Fig. 2A and B).

Table 1
Summary of three-way analyses of variance (F-values) for biomass accumulation, shoot:root ratio, relative root distribution mass ratio, longest root length, total N content, and total P content of *Carex brevicuspis* plants growing in treatments with two water levels, three sediment types, and three plant densities.

Variables	n	Water level (W)	Plant density (D)	Sediment type (S)	S × W	S × D	W × D	S × W × D
Biomass accumulation (g)	5	**90.188*****	**288.292*****	**75.415*****	2.322^{ns}	**6.474*****	**12.466*****	0.781^{ns}
Shoot:root ratio	5	**36.704*****	**38.898*****	**12.325*****	**15.002*****	1.973^{ns}	2.835^{ns}	0.995^{ns}
Relative root distribution mass ratio	5	**110.769*****	**8.911*****	**19.720*****	**22.807*****	**7.197*****	**6.159****	**5.149****
The longest root length (cm)	5	**14.429*****	**4.230***	0.260^{ns}	0.561^{ns}	0.773^{ns}	0.285^{ns}	0.393^{ns}
Total N content (mg g^{-1})	5	0.257^{ns}	0.356^{ns}	**4.008***	**6.977****	**8.645*****	0.257^{ns}	0.503^{ns}
Total P content (mg g^{-1})	5	**32.132*****	1.680^{ns}	1.666^{ns}	**24.474*****	**10.498*****	**6.611****	1.436^{ns}

^{NS} P > 0.05; * P < 0.05; ** P < 0.01; *** P < 0.001.
P < 0.05 for the bold values.

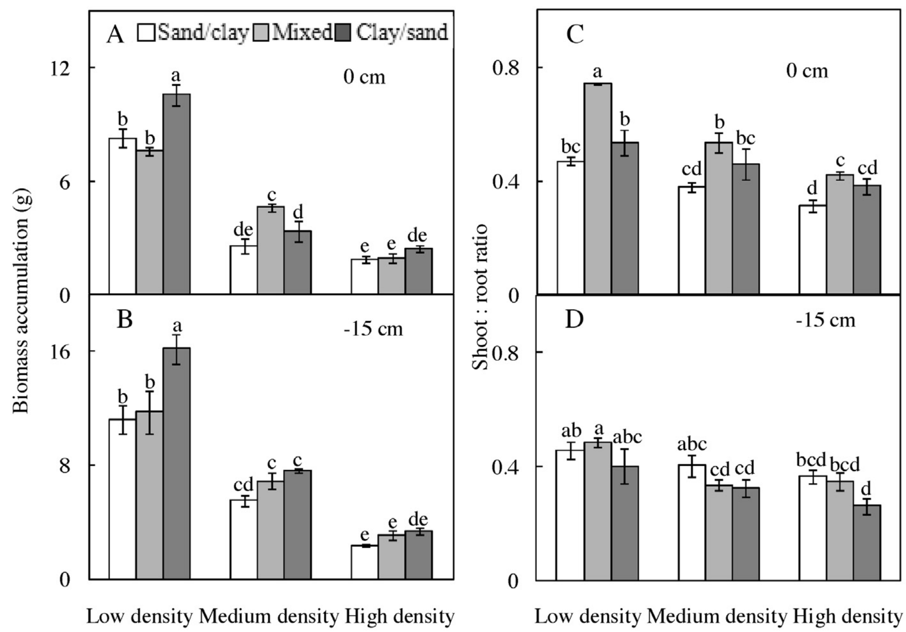

Fig. 2. Biomass accumulation (A and B) and shoot:root ratio (C and D) of *Carex brevicuspis* plants growing in treatments with two water levels, three sediment types (sand/clay; mixed; clay/sand) and three plant densities. Values are means ± SE, with five replications. Different letters indicate a significant difference between treatments at the 0.05 significance level.

3.2. Biomass allocation

Water level, plant density, and sediment type all had a significant effect on the shoot:root ratio (Table 1; Fig. 2C and D), which was markedly higher in the high water level treatments than in the low water level treatments and decreased significantly with increasing plant density. The effect of sediment type on the shoot:root ratio was significant only at the high water level, but not at the low water level. In the high water level, the shoot:root ratio was lower in the sand/clay sediment than in the other two sediment types (Fig. 2C and D).

3.3. Root characteristics

The relative root distribution mass ratio was markedly higher in the high water level treatments than in the low water level treatments (Table 1; Fig. 3A and B). In the high water level treatments, the relative root distribution mass ratio significantly increased with increasing plant density, particularly in the clay/sand sediment and was lower in the sand/clay sediment than in the other two sediment types. In the low water level treatments, the relative root distribution mass ratio did not differ significantly between the investigated plant densities or sediment type (Fig. 3A and B).

The longest root length was significantly higher in the low water level than in the high water level (Table 1; Fig. 3C and D). In the high water level, the longest root length increased with increasing density in the sand/clay sediment treatment. However, in the low water level treatments, the longest root length did not differ significantly between the investigated sediment types and plant densities.

3.4. Total N and P contents

The total N content was significantly influenced only by sediment type and only at low and medium plant densities (Table 1; Fig. 4A and B). In the low plant density treatments, the total N content was significantly higher in the sand/clay sediment than in the other two sediment types; on the other hand, in the medium plant density treatments, it was significantly higher in the clay/sand sediment than in the other two sediment types (Fig. 4A and B).

The total P content was markedly higher in the high water level treatments than in the low water level treatments; however, it did not differ significantly between the investigated sediment types and plant densities (Table 1; Fig. 4C and D). The highest total P content (0.53 ± 0.01 mg·g^{-1}) was observed in the high water level + medium plant density + clay/sand sediment treatment (Fig. 4C and D). This value was 1.36 times higher than the lowest total P content (0.39 ± 0.00 mg g^{-1}), which was observed in the low water level + clay/sand sediment + high plant density treatment (Fig. 4C and D).

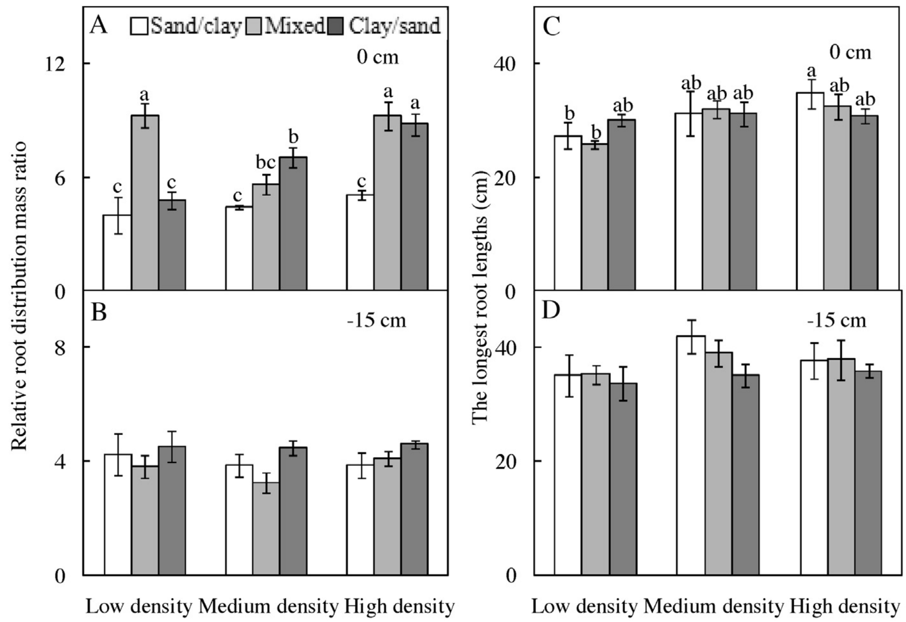

Fig. 3. Relative root distribution mass ratio (A and B) and longest root length (C and D) of *Carex brevicuspis* plants growing in treatments with two water levels, three sediment types (sand/clay; mixed; clay/sand) and three plant densities. Values are means ± SE, with five replications. Different letters indicate a significant difference between treatments at the 0.05 significance level.

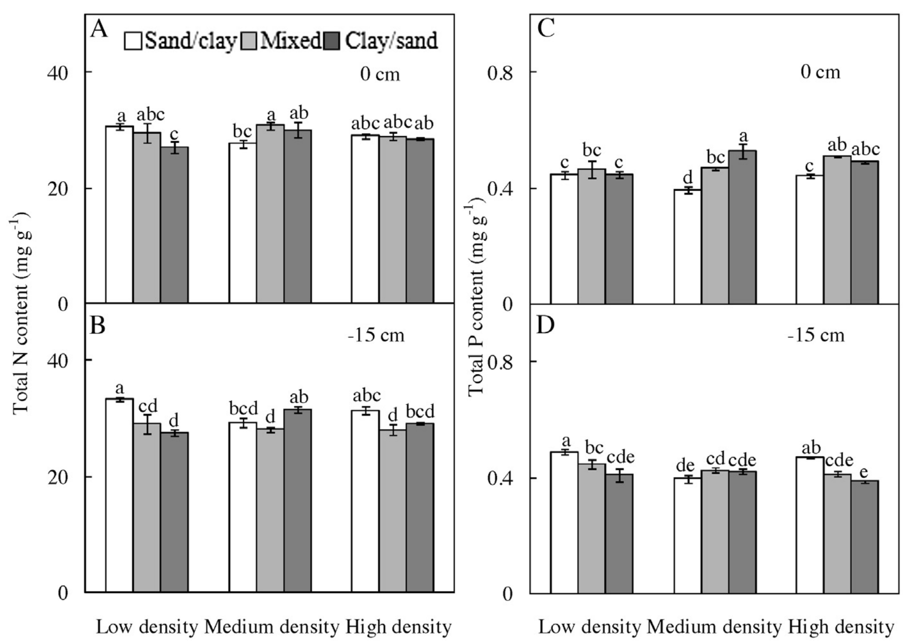

Fig. 4. Total N (A and B) and P (C and D) contents of *Carex brevicuspis* plants growing in treatments with two water levels, three sediment types (sand/clay; mixed; clay/sand) and three plant densities. Values are means ± SE, with five replications. Different letters indicate a significant difference between treatments at the 0.05 significance level.

4. Discussion

Partially consistent with our first prediction, biomass accumulation significantly decreased with increasing plant density and was markedly higher in the low water level treatment than in the high water level treatment. Our results are in accordance with those of a previous study, which showed that *C. brevicuspis* grew better in a −20-cm water level than in 0-cm or 20-cm water levels (Li et al., 2013). *Polygonum hydropiper*—another dominant plant that is usually co-distributed with *C. brevicuspis* in Dongting Lake—also grows better in water-deficit conditions than in a 0-cm water level (Li et al., 2015). The relatively low oxygen availability observed in the high water level treatment may be derived from low biomass accumulation (Chen et al., 2014; Li et al., 2015). On the other hand, the total P content was higher in the high water level than in the low water level. This finding indicates that *C. brevicuspis* roots have high nutrient-absorbing ability, even in water-saturated conditions; hence, this species can acclimate to a variety of water regimes.

The negative effects of plant density on growth are well documented (Lentz, 1999; Li et al., 2014). In our present study, low biomass accumulation in the medium and high plant density treatments may have been caused by intensified competition for limited resources such as light and nutrients (Driever et al., 2005). In general, the highest biomass accumulation occurred in the clay/sand sediment, implying that growth of *C. brevicuspis* is strongly influenced by sediment heterogeneity. This finding confirms our first prediction but not with the results of previous studies. For example, the growth of *Vallisneria natans* and *Prosopis glandulosa* did not differ significantly between various spatial heterogeneity sediments (Maestre and Reynolds, 2006; Xie et al., 2007). Hence, the influence of sediment heterogeneity on plant growth is species-specific, and may be associated with differences in nutrient-obtaining ability between species.

In our present study, the shoot:root ratio was markedly higher in the high water level treatments than in the low water level treatments, indicating that adjustment of biomass allocation enables *C. brevicuspis* to acclimate to water-saturated conditions. Allocating a higher amount of biomass to the shoots maximizes photosynthesis and increases plant survival (Sorrell et al., 2002). Our findings are in agreement with those of previous studies (Luo and Xie, 2009; Romanello et al., 2008). In addition, a decrease in the shoot:root ratio under conditions of high plant density—and therefore strong intraspecific competition— would benefit plants. Therefore, consistent with previous findings, *C. brevicuspis* growth in the present study may have been limited by low nutrient availability (Lentz, 1999; Li et al., 2014). We further found that the shoot:root ratio was significantly lower in the sand/clay sediment than in the other two sediment types; hence, in accordance with a previous study (Xie et al., 2007), when grown in infertile conditions, *C. brevicuspis* allocates a higher amount of biomass to the roots for nutrient capture.

Root growth is highly sensitive to infertile and/or anoxic conditions (Xie et al., 2007). In our present study, we determined a high relative root distribution mass ratio and low longest root length in the high water level treatments. Our findings indicate that *C. brevicuspis* develops a shallow root system in response to flooding conditions. Allocating a larger number of roots to the 0–15-cm layer would increase oxygen acquisition and decrease root oxygen demand (Pan et al., 2014; Li et al., 2015). In the high water level + clay/sand sediment treatments, the relative root distribution mass ratio increased with increasing plant density. The 0–15-cm layer of the clay/sand sediment had high nutrient availability; hence, it is likely that plants allocate higher amounts of root biomass to this layer in order to obtain sufficient nutrients for plant growth. In the sand/clay sediment, the longest root length increased with increasing plant density in the high water level, suggesting that intraspecific competition stimulated root elongation of *C. brevicuspis*, to obtain higher quantities of nutrients. We further found that in the high water level treatments, the relative root distribution mass ratio was lower in the sand/clay sediment than in the other two sediment types. A possible explanation is that plant growth was nutrient limited in the top layer of the sand/clay sediment; hence, *C. brevicuspis* allocated a larger number of roots to the nutrient-enriched layer. However, in our present study, we did not measure the change in sediment nutrient content during the experiment.

Owing to its multiple ecological functions, such as a food resource for migratory birds and a spawning ground for migratory fish, the *C. brevicuspis* community plays an important role in biodiversity maintenance in Dongting Lake. However, recently, the *C. brevicuspis* community has been seriously degraded because of changes in the hydrological regime and anthropogenic disturbance such as livestock grazing, fires, and wheat planting. In our present study, we have demonstrated that *C. brevicuspis* could increase the shoot:root ratio and develop shallow root system to acclimate to high water level and which could adjust shoot:root ratio and root characteristics to acclimate to higher density and sediment heterogeneity conditions such as decreasing shoot:root ratio, allocate more root and increasing root length to the nutrient rich layer. However, besides water level, sediment heterogeneity, and plant density, growth of this species is strongly influenced by other environmental stresses, e.g., grazing, fire, sediment burial, and interspecific competition. Therefore, further studies to determine the effects of these factors on plant growth performance are required.

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References

Blom, C.W.P.M., Voesenek, L.A.C.J., 1996. Flooding: the survival strategies of plants. Trends Ecol. Evol. 11, 290–295.

Chen, X.S., Xie, Y.H., Deng, Z.M., Li, F., Hou, Z.Y., 2011. A change from phalanx to guerrilla growth form is an effective strategy to acclimate to sedimentation in a wetland sedge species *Carex brevicuspis* (Cyperaceae). Flora 206, 347–350.

Chen, X.S., Deng, Z.M., Xie, Y.H., Li, F., Li, X., 2014. Differential growth and vegetative reproduction of two co-occurring emergent macrophytes along a water table gradient. Pak. J. Bot. 46, 881–886.

Dai, L.K., Liang, S.Y., Zhang, S.R., Tang, Y.C., Koyama, T., Tucker, G.C., Simpson, D.A., Noltie, H.J., Strong, M.T., Bruhl, J.J., Wilson, K.L., Muasya, A.M., 2010. Flora of China (Cyperaceae), vol. 23. Science Press Beijing, and Missouri Botanical Garden Press, St. Louis.

Deegan, B.M., White, S.D., Ganf, G.G., 2007. The influence of water level fluctuations on the growth of four emergent macrophyte species. Aquat. Bot. 86, 309–315.

Deng, Z.M., Chen, X.S., Xie, Y.H., Pan, Y., Li, F., Hou, Z.Y., Li, X., Xie, Y.J., 2013. Plasticity of the clonal growth in the wetland sedge *Carex brevicuspis* along a small − scale elevation gradient in Dongting Lake wetlands, China. Ann. Bot. Fennici. 50, 151–159.

Dou, W.F., Wang, H.B., Xu, Y., Xing, W., Liu, G.H., 2010. Effects of water depth and substrate type on growth dynamics and biomass allocation of *Oryza rufipogon*. Acta Ecol. Sin. 30, 16–21.

Driever, S.M., Nes, E.H.V., Roijackers, R.M.M., 2005. Growth limitation of *Lemna minor* due to high plant density. Aquat. Bot. 81, 245–251.

Frank, S.J., Peterson, C.J., 2003. Burial disturbance leads to facilitation among coastal dune plants. Plant Ecol. 168, 13–21.

Klump, J.V., Martens, C.S., 1989. The seasonality of nutrient regeneration in an organic-rich coastal sediment-kinetic modeling of changing pore-water nutrient and sulfate distributions. Limnol. Oceanogr. 34, 559–577.

Lentz, K.A., 1999. Effects of intraspecific competition and nutrient supply on the endangered Northeastern bulrush, *Scirpus ancistrochaetus* Schuyler (Cyper-aceae). Am. Midl. Nat. 142, 47–54.

Li, H.L., Zhi, Y.B., An, S.Q., Zhao, L., Zhou, C.F., Deng, Z.F., Gu, S.P., 2009. Density − dependent effects on the dieback of exotic species *Spartina anglica* in coastal China. Ecol. Eng. 35, 544–552.

Li, F., Qin, X.Y., Xie, Y.H., Chen, X.S., Hu, J.Y., Hou, Z.Y., 2013. Physiological mechanisms for plant different distribution patterns: responses of three typical wetland plants to flooding and drought in the Dongting Lake. Liminology 14, 71–76.

Li, F., Xie, Y.H., Tang, Y., Liu, Y.Y., Chen, X.S., Deng, Z.M., Hu, J.Y., Liu, N., 2014. Negative influence of burial stress on plant growth was ameliorated by increased plant density in *Polygonum hydropiper*. Limnologica 45, 33–37.

Li, F., Yang, G., Xie, Y.H., Chen, X.S., Deng, Z.M., Hu, J.Y., 2015. Competition in two wetland macrophytes in response to drained and waterlogged soil conditions. J. Liminol. 74, 623–630.

Luo, W.B., Xie, Y.H., 2009. Growth and morphological responses to water level and nutrient supply in three emergent macrophyte species. Hydrobiologia 624, 151–160.

Luo, W.B., Xie, Y.H., Chen, X.S., Li, F., Qin, X.Y., 2010. Competition and facilitation in three marsh plants in response to a water − level gradient. Wetlands 30, 525–530.

Maestre, F.T., Reynolds, J.F., 2006. Small-scale spatial heterogeneity in the vertical distribution of soil nutrients has limited effects on the growth and development of *Prosopis glandulosa* seedlings. Plant Ecol. 183, 65–75.

Pagter, M., Bragato, C., Brix, H., 2005. Tolerance and physiological responses of *Phragmites australis* to water deficit. Aquat. Bot. 81, 285–299.

Pan, Y., Xie, Y.H., Deng, Z.M., Tang, Y., Pan, D.D., 2014. High water level impedes the adaptation of *Polygonum hydropiper* to deep burial: responses of biomass allocation and root morphology. Sci. Rep. 4, 5612.

Parolin, P., Lucas, C., Piedade, M.T.F., Wittmann, F., 2010. Drought responses of flood – tolerant trees in Amazonian floodplains. Ann. Bot. 105, 129–139.
Retuerto, R., Rochefort, L., Woodward, F.I., 1996. The influence of plant density on the responses of *sinapis alba* to CO_2 and windspeed. Oecologia 108, 241–251.
Romanello, G.A., Chuchra-Zbytniuk, K.L., Vandermer, J.L., Touchette, B.W., 2008. Morphological adjustments promote drought avoidance in the wetland plant *Acorus americanus*. Aquat. Bot. 89, 390–396.
Shi, R.H., 1994. Agricultural and Chemical Analysis for Soil. Chinese Agriculture Press (in Chinese), Beijing.
Shilo-Volin, H., Novoplansky, A., Goldberg, D.E., Turkington, R., 2005. Density regulation in annual plant communities under variable resource levels. Oikos 108, 241–252.
Sorrell, B.K., Tanner, C.C., Sukias, J.P.S., 2002. Effects of water depth and substrate on growth and morphology of *Eleocharis sphacelata*: implications for stem support and internal gas transport. Aquat. Bot. 73, 93–106.
Wetzel, P.R., van der Valk, A.G., 1998. Effects of nutrient and soil moisture on competition between *Carex stricta*, *Phalaris arundinacea*, and *Typha latifolia*. Plant Ecol. 138, 179–190.
Xie, Y.H., Deng, W., Wang, J.D., 2007. Growth and root distribution of *Vallisneria natans* under heterogeneous sediment environments. Aquat. Bot. 86, 9–13.
Xie, Y.H., Ren, B., Li, F., 2009. Increased nutrient supply facilitates acclimation to high water level in the marsh plant *Deyeuxia angustifolia*: the response of root morphology. Aquat. Bot. 91, 1–5.