

# Growth and morphological responses to water level and nutrient supply in three emergent macrophyte species

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**Abstract** Sanjiang Plain is the largest freshwater marsh in China, where plant zonation along water-level gradients is a common phenomenon. The aim of this experiment was to identify the role of water level and nutrient availability on plant zonation in the plain. Growth and root morphology of three perennial emergent macrophyte species were investigated by growing in two water levels (0.1 and 10.0 cm, relative to soil surface) and in two levels of nutrient supply (0 and 0.5 g slow-release fertilizer per container). In the plain, *Carex lasiocarpa* typically occurs at low elevations, *Glyceria spiculosa* at medial elevations, and *Deyeuxia angustifolia* at high elevations. The relative growth rate was the highest in *C. lasiocarpa* and the lowest in *D. angustifolia* in the 10.0-cm water level. Among the three species, only total biomass of *D. angustifolia* was affected by water level, and decreased with increasing water level. High nutrient supply led to increased total biomass in

*C. lasiocarpa* and *G. spiculosa*. High water level led to an increased root diameter in *G. spiculosa* and a decreased root length in *C. lasiocarpa*. In the 10.0-cm water level, low nutrient supply led to thinner roots in *D. angustifolia*, but resulted in an increased specific root length (SRL) in *C. lasiocarpa* and root diameter in *G. spiculosa*. Water-level effect on root porosity was only observed in *G. spiculosa*, and nutrient amendment did not influence root porosity in all the species. These data indicate that both nutrient and water level are important factors regulating plant distribution pattern in the Sanjiang Plain, because both *C. lasiocarpa* and *G. spiculosa* are relatively sensitive to nutrient supply whereas *D. angustifolia* is sensitive to water level.

**Keywords** Flooding · Nutrient availability · Plant growth · Root morphology · Root porosity

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## Introduction

Sanjiang Plain is the largest freshwater marsh in China, about 108,900 km<sup>2</sup> (Ma, 1995), which is deposited by Songhua River, Heilong River, and Wusuli River. In the plain, distinct plant zonation along water-level gradients is a common phenomenon (Yi et al., 1985). In a typical site, *Carex lasiocarpa* and *C. pseudocuraica* usually distribute at relatively low elevations, *Glyceria spiculosa*,

*C. limosa* and *C. meyeriana* at the medial elevations, and *Deyeuxia angustifolia* at high elevations (Yi et al., 1985). However, the mechanism accounting for plant zonation in the plain is still unclear.

Earlier studies have shown that flooding is a primary factor determining plant zonation due to anoxia and reduced Eh in the soil (Jackson & Drew, 1984; Drew, 1997). As a result, differences in tolerance to flooding may determine where plants are distributed. For flood-tolerant species, resistance to soil-oxygen deficiency can be achieved via morphological adjustments, such as thick and unbranched roots with developed aerenchyma (Laan & Blom, 1990), shallow root systems, and reduced root:shoot ratio (Kozłowski, 1984; Rubio et al., 1995; Blom & Voeselek, 1996; Pezeshki et al., 1996). These changes are beneficial for plant adaptation to soil flooding, by increasing oxygen transport to roots or by reducing radial oxygen loss to the soil (Blom et al., 1990; Blom & Voeselek, 1996; Naidoo & Naidoo, 1992).

Nutrient is another limiting factor influencing the growth and distribution of wetland plants. Nutrients, especially for nitrogen, are highly dependent on soil moisture levels, and dry soil is usually concomitant with nutrient deficiency (Bonetto et al., 1994; Rejmánková et al., 1996). Studies have shown that N and P levels limit species distribution in some wetlands (Verhoeven & Schmitz, 1991). Increased nutrient input from agricultural, urban, or atmospheric sources has caused the alteration of structure and composition in wetland plant community worldwide (Bedford et al., 1999; Johnson, 2004). Wheeler (1999) suggested that enhanced nutrient supply might counteract the negative effects of flooding on plant growth for the fast growing species. Therefore, studies of the interactions between nutrient availability and water level are significant (Emery et al., 2001).

The aim of this experiment was to identify the role of water level and nutrient availability on plant zonation in the Sanjiang Plain, by investigating plant growth and root morphology. To this end, three dominant perennial emergent macrophytes in the plain distributed in different elevations along a water-level gradient (low-elevation species *C. lasiocarpa*, med-elevation species *G. spiculosa*, and high-elevation species *D. angustifolia*) were chosen to grow in two water levels and in two levels of nutrient supply

to test for the following hypotheses. First, growth and root morphology will be more dramatically affected by water level in the high-elevation species *D. angustifolia* than in the low-elevation species *C. lasiocarpa*, because the former species has less opportunity facing flooding events than the latter. Secondly, growth and root morphology are more sensitive to nutrient availability in the low-elevation species *C. lasiocarpa* than in the high-elevation species *D. angustifolia* because *C. lasiocarpa* usually grows in inundated and nutrient-rich soils.

## Materials and methods

### Plant materials

Representative individuals of *C. lasiocarpa*, *G. spiculosa*, and *D. angustifolia* were chosen in October 2005, from Sanjiang Freshwater Marsh Field Observation Station (N 47°35', E 133°31'), the Chinese Academy of Sciences. The plants were cut into small blocks (15 cm × 15 cm × 20 cm), and transported to a greenhouse in the Northeast Institute of Geography and Agricultural Ecology, the Chinese Academy of Sciences, where the temperature was controlled at 25 ± 2°C in the day and 17 ± 2°C at night and the light was provided by 400-watt SON-T ARGO sodium lamps (Philip, Guildford, UK) at a photon flux density of 600 μmol m<sup>-2</sup> s<sup>-1</sup> (PPAR) in a 14-h light/10-h dark cycle. Plant cuttings were then placed into plastic buckets, which contained 10-cm soil and 2-cm water, to germinate new ramets.

### Experimental design

Two months after establishment in the greenhouse, young plants (3–4 leaves, about 20 cm in height) were selected and planted in plastic containers (12 cm in height and 15 cm in diameter, one plant per container), which were filled with 20:80 (v/v) mixtures of soil and sand. The mixture contained 0.6% organic matter, 40.5 μg g<sup>-1</sup> exchangeable N, and 16.1 μg g<sup>-1</sup> exchangeable P. The soil was collected from the relatively high-elevation sites (N 47°35.001' E 133°30.202') in the Sanjiang Freshwater Marsh Field Observation Station, and the sand was collected from a local river (Yitong River). Each container was placed into one bigger plastic bucket

(30 × 40 × 40 cm) to control water level. The treatments combined two levels of nutrient supply with two water levels in a factorial (nutrient × water) design, with four replicates. Two levels of nutrient supply were 0 and 0.5 g slow-release fertilizer (N-P-K: 23-10-12) per container, and two water levels were 0.1 and 10.0 cm, relative to the soil surface (remaining 12.1-cm and 22-cm water level in the bucket, respectively). Tap water (containing 4.3 μM NH<sub>4</sub><sup>+</sup>-N, 16.8 μM NO<sub>3</sub>-N and 1.9 μM PO<sub>4</sub><sup>3-</sup>-P) was supplied as needed to control water level. Slow-release fertilizer, soil, and sand were thoroughly mixed.

#### Harvest and root morphology

The plants were harvested after 16 weeks. After removal from the soil, plants were carefully cleaned by tap water, and divided into shoots and roots, and fresh weights recorded. The roots were placed in plastic trays with water to preserve the structure. Fresh weights of about half of each tissue type were recorded, oven dried at 80°C for 48 h, and then weighted again to calculate a wet-to-dry conversion for each tissue type. The dry weights were used for calculation. The remaining root tissues were used for measurement of root morphology and porosity. For each treatment, 2–3 representative adventitious roots per plant were chosen to measure root length, and the average was recorded. The diameter was calculated using a microscope with an ocular micrometer (Xie et al., 2005). We randomly chose 7–8 roots per plant for measurement and averaged. Two adventitious roots per plant were randomly chosen as a group for measuring root length and root mass, and Specific root length (SRL) was calculated as the ratio of root length to root mass.

Relative growth rate (RGR) was calculated using the equation:

$$\text{RGR} = (\ln w_2 - \ln w_1) / (t_2 - t_1),$$

where  $w_2$  and  $w_1$  indicated the final and initial plant dry weight, respectively, and  $(t_2 - t_1)$  indicated the experimental time (days). At the beginning of the experiment, six plants per species, similar to the plants planted in the containers, were oven dried at 80°C for 48 h, and dry weight was recorded as the initial biomass.

#### Root porosity

Adventitious roots from different treatments were examined for porosity (percentage of air-filled volume) by the pycnometer method (Jensen et al., 1969). Root porosity is usually used as an indicator of the capacity of the lacunar system to deliver oxygen to below-ground tissues. Representative fresh adventitious roots (more than 5 cm) from different plants were removed intact, and were separated into roots and laterals by a nipper. Adventitious roots were cut into 1–2 mm segments. Root porosity was then determined using 0.1–0.3 g of root tissue and a 25-ml pycnometer. Three determinants per treatment were made using a vacuum pump.

#### Statistical analysis

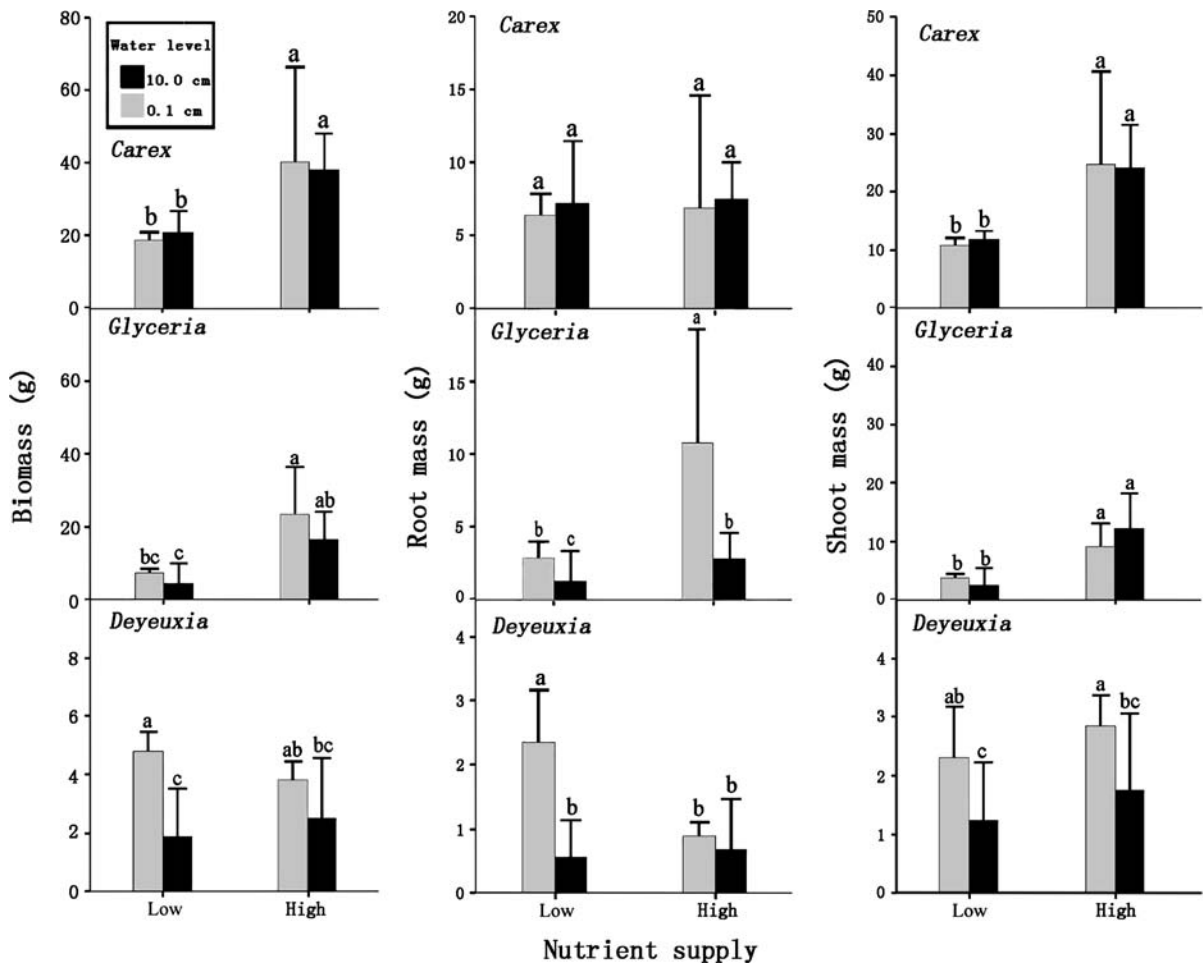
Two-way ANOVAs, with water level and nutrient supply as main factors, were performed to determine main effects and interactions on total biomass, biomass allocation, and root characteristics. Multiple comparisons of means were performed by Duncan's test at the 0.05 significance level. Data were log<sub>10</sub>-transformed if necessary to reduce heterogeneity of variances, and homogeneity was tested using Levene's test.

## Results

#### Total biomass

Among the three species, the total biomass was the highest in *C. lasiocarpa* (19–39 g per plant), intermediate in *G. spiculosa* (5–17 g per plant), and the lowest in *D. angustifolia* (2–5 g per plant). Enhanced water level did not influence total biomass of *C. lasiocarpa* and *G. spiculosa* ( $P > 0.05$ , Fig. 1), but reduced total biomass of *D. angustifolia* in the low nutrient supply ( $P < 0.001$ , Fig. 1). Shoot mass (Fig. 1) and RGR (Fig. 2) showed the same tendency as total biomass. Enhanced water level had no effects on root mass of *C. lasiocarpa* or *D. angustifolia* at high nutrient supply ( $P > 0.05$ , Fig. 1), but led to a decreased root mass in *G. spiculosa* ( $P < 0.001$ , Fig. 1).

Nutrient supply did not influence total biomass of *D. angustifolia* ( $P > 0.05$ , Fig. 1, Table 1), whereas



**Fig. 1** Total biomass, Shoot mass and root mass (means  $\pm$  SE,  $n = 4$ ) of *C. lasiocarpa* (*Carex*), and *G. spiculosa* (*Glyceria*), and *D. angustifolia* (*Deyeuxia*) growing in two

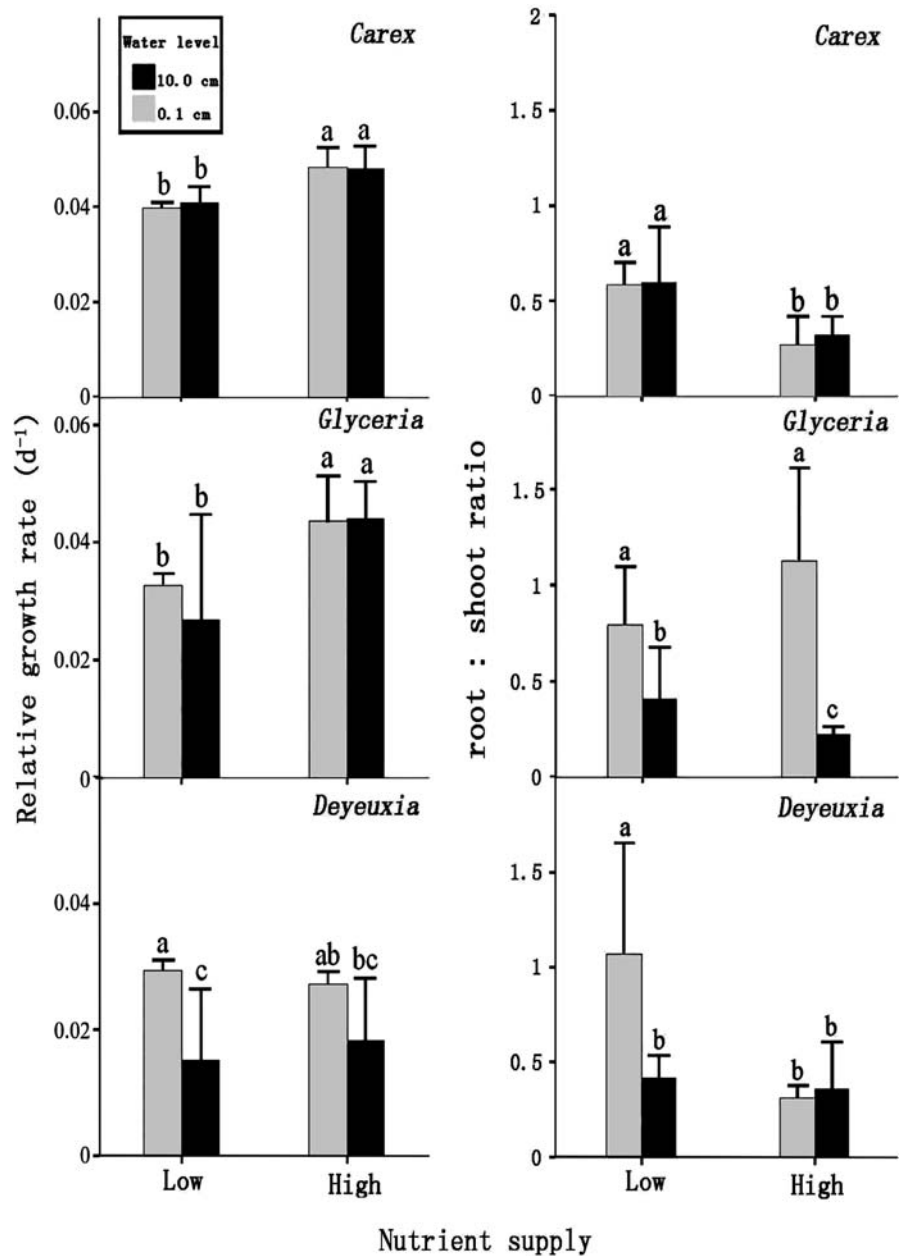
water levels and two levels of nutrient supply. Low and High indicate 0 and 0.5 g fertilizer per container. Different letters indicate significant differences among treatments ( $P < 0.05$ )

total biomass increased with increasing nutrient supply in *C. lasiocarpa* and *G. spiculosa* ( $P > 0.05$ , Fig. 1). Shoot mass and RGR showed the same tendency as total biomass. Root mass was unaffected by nutrient supply in *C. lasiocarpa* and *D. angustifolia* in the 10.0-cm water level ( $P > 0.05$  Table 1, Figs. 1, 2). However, root mass of *G. spiculosa* was lower at low nutrient supply ( $P < 0.001$ , Table 1, Fig. 1). The effects of water level on root mass of *D. angustifolia* were dependent on nutrient supply (significant water  $\times$  nutrient interaction,  $P < 0.05$ , Table 1). These data suggested that *D. angustifolia* is relatively sensitive to flooding, whereas both *G. spiculosa* and *C. lasiocarpa* are sensitive to nutrient supply.

#### Biomass allocation

Both water level and nutrient supply had significant effects on root:shoot ratios of *G. spiculosa* and *D. angustifolia* ( $P < 0.05$ , Table 1), whereas biomass allocation of *C. lasiocarpa* was only affected by nutrient supply ( $P < 0.001$ , Fig. 2). Under low nutrient conditions, enhanced water level led to reduced root: shoot ratios of *G. spiculosa* and *D. angustifolia* ( $P < 0.05$ , Fig. 2). The effect of nutrient supply on biomass allocation in *G. spiculosa* was dependent on water level (significant water  $\times$  nutrient interaction,  $P < 0.05$ , Table 1). Root:shoot ratios of *C. lasiocarpa* and *G. spiculosa* were higher at low nutrient supply in

**Fig. 2** Relative growth rate ( $d^{-1}$ ) (means  $\pm$  SE,  $n = 4$ ) and root:shoot ratio (means  $\pm$  SE,  $n = 4$ ) of *C. lasiocarpa* (*Carex*), *G. spiculosa* (*Glyceria*) and *D. angustifolia* (*Deyeuxia*) growing in two water levels and two levels of nutrient supply. Low and High indicate 0 and 0.5 g fertilizer per container. Different letters indicate significant differences among treatments ( $P < 0.05$ )



the 10.0-cm water level ( $P < 0.05$ , Fig. 2), whereas low nutrient supply led to a higher root:shoot ratio of *D. angustifolia* in the 0.1-cm water level ( $P < 0.05$ , Fig. 2).

#### Root characteristics

Enhanced water level did not influence root diameter of *C. lasiocarpa* and *D. angustifolia* at high nutrient supply ( $P > 0.05$ , Fig. 3), but led to an increased root

diameter in *G. spiculosa* ( $P < 0.05$ , Fig. 3). Both water level and nutrient amendment interacted to influence root diameter and SRL of *D. angustifolia* ( $P < 0.05$ , Table 1, Fig. 4). Low nutrient supply resulted in an increased SRL in *C. lasiocarpa* in the 0.1-cm water level and in *G. spiculosa* in the 10.0-cm water level ( $P < 0.05$ , Fig. 4). For *C. lasiocarpa* and *D. angustifolia*, a thicker root was observed at high nutrient supply ( $P < 0.05$ , Fig. 3). However, low nutrient supply increased root diameter of *G. spiculosa*

**Table 1** Summary of two-way ANOVAs for plant biomass, shoot and root mass and root characteristics of *C. lasiocarpa* (*Carex*), *G. spiculosa* (*Glyceria*) and *D. angustifolia* (*Deyeuxia*) growing in two water levels and two levels of nutrient supply (*F*-values)

	Species	<i>n</i>	Nutrient ( <i>N</i> )	Water ( <i>W</i> )	<i>N</i> × <i>W</i>
Biomass mass (g)	<i>Carex</i>	4	48.18 <sup>***</sup>	0.06 <sup>ns</sup>	0.55 <sup>ns</sup>
	<i>Glyceria</i>	4	23.85 <sup>***</sup>	4.40 <sup>ns</sup>	0.74 <sup>ns</sup>
	<i>Deyeuxia</i>	4	0.06 <sup>ns</sup>	16.21 <sup>**</sup>	1.90 <sup>ns</sup>
Root mass (g)	<i>Carex</i>	4	0.60 <sup>ns</sup>	2.13 <sup>ns</sup>	0.02 <sup>ns</sup>
	<i>Glyceria</i>	4	11.00 <sup>**</sup>	12.52 <sup>**</sup>	0.00 <sup>ns</sup>
	<i>Deyeuxia</i>	4	10.77 <sup>**</sup>	24.55 <sup>***</sup>	15.38 <sup>**</sup>
Shoot mass (g)	<i>Carex</i>	4	64.54 <sup>***</sup>	0.13 <sup>ns</sup>	0.39 <sup>ns</sup>
	<i>Glyceria</i>	4	31.10 <sup>***</sup>	0.40 <sup>ns</sup>	3.39 <sup>ns</sup>
	<i>Deyeuxia</i>	4	3.04 <sup>ns</sup>	12.96 <sup>**</sup>	0.00 <sup>ns</sup>
Root:Shoot ratio	<i>Carex</i>	4	28.07 <sup>***</sup>	0.25 <sup>ns</sup>	0.13 <sup>ns</sup>
	<i>Glyceria</i>	4	0.56 <sup>ns</sup>	60.11 <sup>***</sup>	9.46 <sup>*</sup>
	<i>Deyeuxia</i>	4	14.41 <sup>**</sup>	5.06 <sup>*</sup>	6.43 <sup>*</sup>
Relative growth rate (d <sup>-1</sup> )	<i>Carex</i>	4	49.85 <sup>***</sup>	0.16 <sup>ns</sup>	0.37 <sup>ns</sup>
	<i>Glyceria</i>	4	20.03 <sup>***</sup>	3.87 <sup>ns</sup>	0.84 <sup>ns</sup>
	<i>Deyeuxia</i>	4	0.14 <sup>ns</sup>	14.50 <sup>**</sup>	1.6 <sup>ns</sup>
Root diameter (mm)	<i>Carex</i>	4	3.43 <sup>ns</sup>	0.28 <sup>ns</sup>	2.82 <sup>ns</sup>
	<i>Glyceria</i>	4	21.88 <sup>***</sup>	13.37 <sup>**</sup>	0.12 <sup>ns</sup>
	<i>Deyeuxia</i>	4	0.46 <sup>ns</sup>	11.21 <sup>**</sup>	14.89 <sup>**</sup>
Root length (cm)	<i>Carex</i>	4	0.40 <sup>ns</sup>	57.01 <sup>***</sup>	2.34 <sup>ns</sup>
	<i>Glyceria</i>	4	0.63 <sup>ns</sup>	1.74 <sup>ns</sup>	2.93 <sup>ns</sup>
	<i>Deyeuxia</i>	4	0.32 <sup>ns</sup>	0.20 <sup>ns</sup>	2.81 <sup>ns</sup>
Root porosity (%)	<i>Carex</i>	3	0.02 <sup>ns</sup>	0.13 <sup>ns</sup>	1.84 <sup>ns</sup>
	<i>Glyceria</i>	3	4.91 <sup>ns</sup>	20.78 <sup>**</sup>	0.40 <sup>ns</sup>
	<i>Deyeuxia</i>	3	1.41 <sup>ns</sup>	0.01 <sup>ns</sup>	2.05 <sup>ns</sup>
Specific root length (cm g <sup>-1</sup> )	<i>Carex</i>	4	2.45 <sup>ns</sup>	16.12 <sup>**</sup>	3.21 <sup>ns</sup>
	<i>Glyceria</i>	4	3.78 <sup>ns</sup>	0.06 <sup>ns</sup>	1.25 <sup>ns</sup>
	<i>Deyeuxia</i>	4	0.48 <sup>ns</sup>	32.51 <sup>***</sup>	21.52 <sup>***</sup>

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ;  
\*\*\*  $P < 0.001$ ; ns  $P > 0.05$

and *D. angustifolia* in the 0.1-cm water level ( $P < 0.05$ , Fig. 3), but led to a decreased root diameter of *D. angustifolia* in the 10.0-cm water level ( $P < 0.05$ , Fig. 3).

Among the three species, root porosity was the highest in *C. lasiocarpa* (26%), intermediate in *G. spiculosa* (20%) and the lowest in *D. angustifolia* (13%). Water-level effect on root porosity was only observed in *G. spiculosa* ( $P < 0.01$  Table 1, Fig. 4). Nutrient amendment did not influence root porosity in all species ( $P > 0.05$  Table 1, Fig. 4).

## Discussion

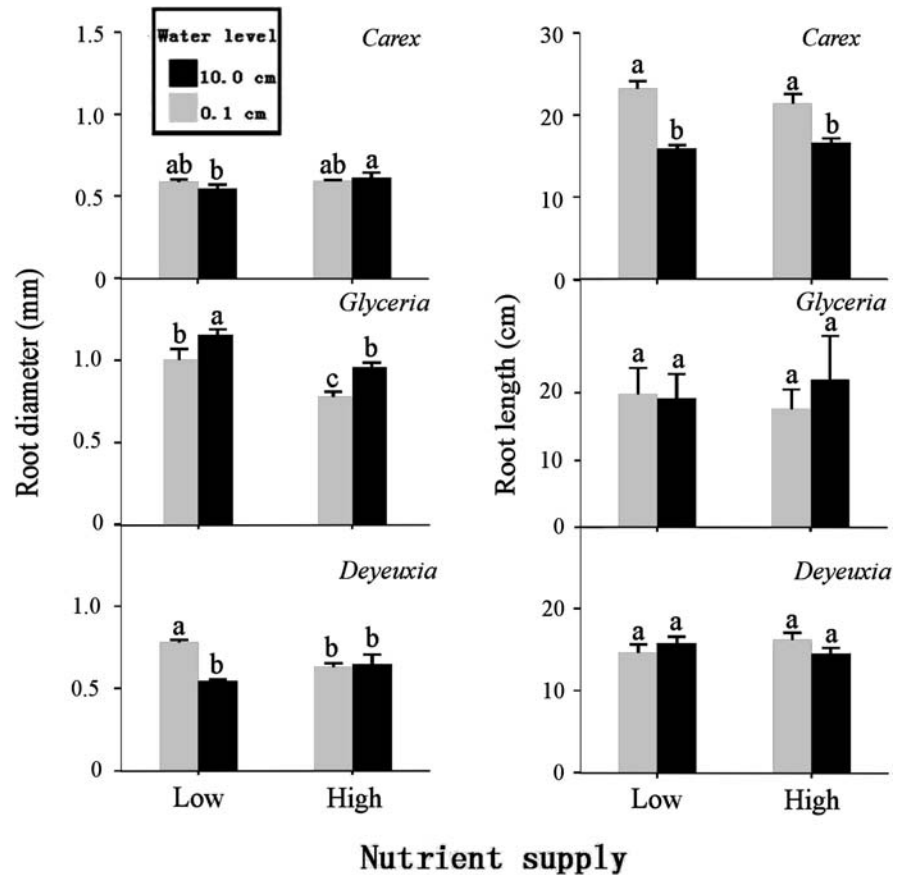
Growth responses in wetland plants to flooding might be species-specific. In support of our prediction, high water level restrained plant growth in *D. angustifolia*,

a finding that is consistent with other studies (Neill, 1990; Edwards et al., 2003). In addition, we also found that total biomass of *C. lasiocarpa* as well as *G. spiculosa* was unaffected by water level.

High growth rate is an advantage to rapidly occupy the limited space and to acquire more resources (Nichole & Biondini, 2002; Mediavilla & Escudero, 2003). For *C. lasiocarpa*, total biomass and biomass allocation were unaffected by water level, which is consistent with the study performed by Lauchlan & Karnezis (2005). The highest RGR in the 10.0-cm water level might support the field observation that *C. lasiocarpa* is dominant in inundated environments. For *D. angustifolia*, high water level reduced root and shoot mass. These data indicate that the competitive ability among the three species might be the highest in *C. lasiocarpa*, and the lowest in *D. angustifolia* in the high water level.



**Fig. 3** Root diameter (means  $\pm$  SE,  $n = 4$ ) and root length (means  $\pm$  SE,  $n = 4$ ) of *C. lasiocarpa* (*Carex*), *G. spiculosa* (*Glyceria*) and *D. angustifolia* (*Deyeuxia*) growing in two water levels and two levels of nutrient supply. Low and High indicate 0 and 0.5 g fertilizer per container. Different letters indicate significant differences among treatments ( $P < 0.05$ )

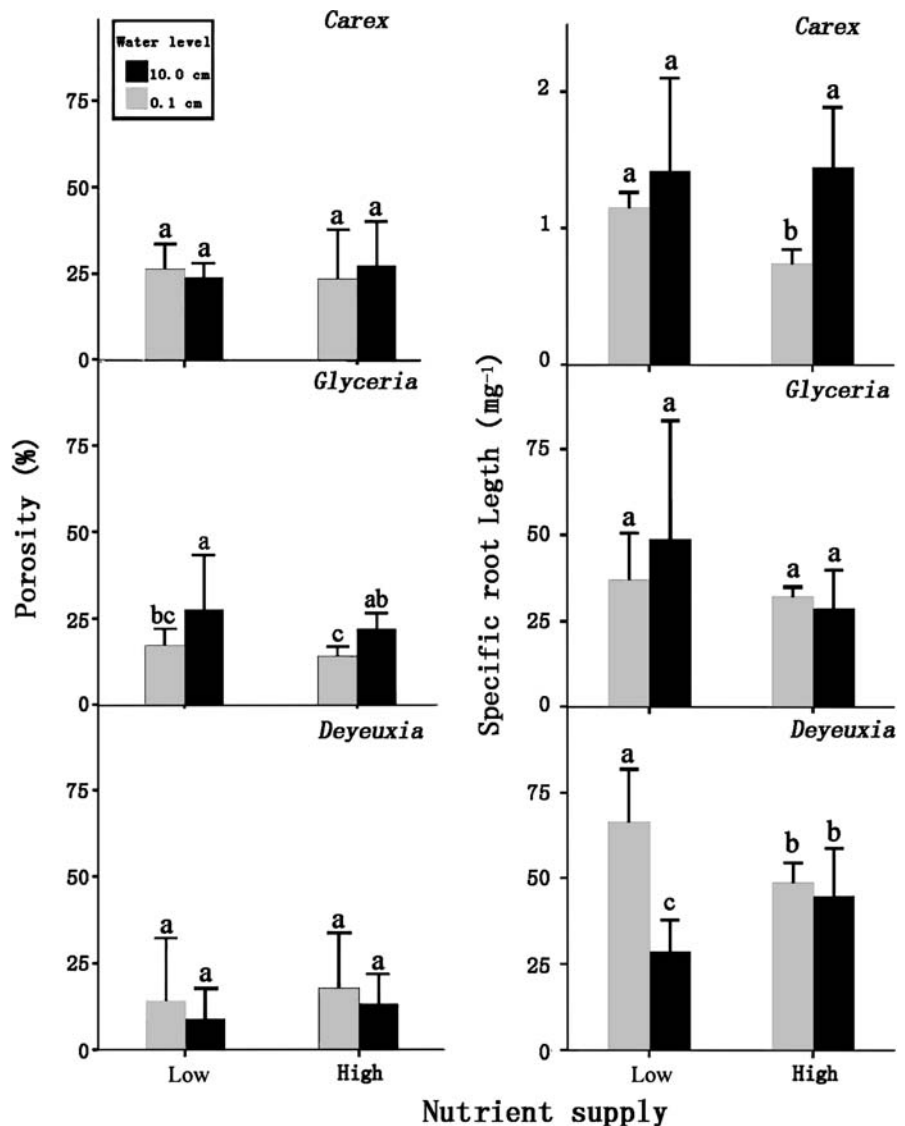


In flooding conditions, increased root diameter, SRL, and root porosity are important adaptive adjustments to enhance root aeration in anoxic environments (Laan & Blom, 1990). In this experiment, root porosity of *C. lasiocarpa* was 26%, which was significantly higher than those of *D. angustifolia* (13%) and *G. spiculosa* (20%). Maybe 10.0-cm water level was insufficient to induce the change of root aerenchyma in *C. lasiocarpa*, as suggested by the unchanged root porosity. Decreased root length of *C. lasiocarpa* in the high water level might reduce the depth of root distribution, and more roots might be distributed in the oxygen-abundant top layer of the soil (Kozłowski, 1984), so *C. lasiocarpa* is more suitable to grow in high water-level environments, where the typical characteristic is permanent inundation. For *G. spiculosa*, increased root diameter, SRL and root porosity in the 10.0-cm water level indicated that this species was the most plastic of the species and that it can adapt rapidly to changed water level. Therefore, *G. spiculosa* is more suitable to grow in

intermediate water-level environments, where the typical characteristic is the alternation of dry and inundation. However, lowest root porosity indicates that the capacity of oxygen transportation in *D. angustifolia* is limited, as suggested by Xie et al. (2008). Enhanced water level led to a thinner root and a lower SRL of *D. angustifolia* at low nutrient supply, which is unfavorable to alleviate the stress of high water level since thinner roots could hamper root function in aeration due to undeveloped aerenchyma (Fitter, 1996). Therefore, these data suggest that *D. angustifolia* is relatively sensitive to water level and both *C. lasiocarpa* and *G. spiculosa* are relatively tolerant to water level.

Total biomass of *C. lasiocarpa* and *G. spiculosa* increased with enhanced nutrient supply, which is consistent with the study performed by Sabine (2005). Root and shoot mass increased at high nutrient supply, and resulted in a higher total biomass in *G. spiculosa*. For *C. lasiocarpa*, only high shoot mass accounted for the increase of total biomass at

**Fig. 4** Specific root length (means  $\pm$  SE,  $n = 4$ ) and porosity (means  $\pm$  SE,  $n = 3$ ) of *C. lasiocarpa* (*Carex*), *G. spiculosa* (*Glyceria*) and *D. angustifolia* (*Deyeuxia*) growing in two water levels and two levels of nutrient supply. Low and High indicate 0 and 0.5 g fertilizer per container. Different letters indicate significant differences among treatments ( $P < 0.05$ )



high nutrient supply. For *D. angustifolia*, nutrient supply had insignificant effects on root, shoot mass and total biomass. Thereby, these data support our hypothesis 2, which predicts that growth of *C. lasiocarpa* is more sensitive to nutrient availability than that of *D. angustifolia*. Dry soil is usually concomitant with nutrient deficiency (Bonetto et al., 1994; Rejmánková et al., 1996), as suggested by the lowest soil total N and total P contents in *D. angustifolia* community (Liu et al., 2005). Therefore, the high-elevation species *D. angustifolia* might face the stress of nutrient deficiency more frequently than *C. lasiocarpa* and *G. spiculosa*. When nutrients

are limiting, more biomass is allocated to root system to increase nutrient acquisition by increasing root-soil contact (Mc Connaughay & Coleman, 1999; Xie et al., 2007), as suggested by a high root: shoot ratio of *D. angustifolia* in the 0.1-cm water level. These data also suggest that *D. angustifolia* may be a better competitor for nutrients than the other species. For *D. angustifolia*, high nutrient supply led to an increased root diameter but an unaltered root mass at high water level, indicating that more oxygen could be transported to the roots to reduce the negative effects of oxygen deficiency. Therefore, these data supported the statement that enhanced nutrient supply



might counteract the negative effects of flooding on the growth of the high-elevation species *D. angustifolia* (Wheeler, 1999).

Agricultural production has increased in the Sanjiang Plain in recent years with an associated increase in groundwater withdrawals for irrigation, which resulted in a decline in wetland water levels and in an increase in nutrient availability (Ma et al., 2001; Wang & Tian, 2003; Wang et al., 2004; Ji & Luan, 2006). In this experiment, reduced water level significantly stimulated the growth of *D. angustifolia*, and total biomass of *C. lasiocarpa* and *G. spiculosa* increased at high nutrient supply, indicating that both water-level and nutrient availability are important factors regulating plant distribution pattern. In the plain, average soil N and P contents of *C. lasiocarpa* and *G. spiculosa* communities were relatively higher than those of *D. angustifolia* community in the dry season (Liu et al., 2005). The appropriate water level for the growth of *D. angustifolia* and *C. lasiocarpa* was 0 cm and 10–30 cm, respectively (Ji et al., 2004, 2006), suggesting that declining water level would result in degradation of the *C. lasiocarpa* community. Field observation has confirmed that degradation of *C. lasiocarpa* was most serious (Ji et al., 2004). These data suggest that appropriate water-level management as well as limitation of agricultural development is important for the marsh protection of Sanjiang Plain. Field observation also indicated that *D. angustifolia* community has declined due to shrub invasion during the last 30 years (Ji et al., 2006). Therefore, biotic interactions are also probably important in determining plant zonation in the Sanjiang Plain, because competition capability might also differ among the three species due to different growth capacities.

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