

Plant distribution can be reflected by the different growth and morphological responses to water level and shade in two emergent macrophyte seedlings in the Sanjiang Plain

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Abstract In the Sanjiang Plain (North East China), narrowleaf small reed (*Deyeuxia angustifolia*) usually distributes widely in typical meadow or marsh, while reed (*Phragmites australis*), the concomitant species, is distributed sparsely in the *D. angustifolia* communities or relative open sites. To date, the mechanisms responsible for their different distribution patterns are far from clear. Both water level and light are important factors determining plant distribution in wetland ecosystems and therefore, the aim of this paper was to identify the role of these two factors and their potential interaction on plant distribution in this plain. Growth responses and biomass allocation of the two macrophytes were investigated by growing

them in three irradiances (300, 100, 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and two water levels (0 and 5 cm) under greenhouse conditions. Biomass accumulation, mean relative growth rate (RGR), height and mean relative elongation rate (RER) of both species significantly decreased with the reduction of light availability. Biomass accumulation, RGR, height and RER of *P. australis* were significantly inhibited by higher water level. However, water level had no effect on the growth of *D. angustifolia*. Stem mass fraction was higher at 0-cm water level in *D. angustifolia*, and was not affected by water level in *P. australis*. These data suggest that *D. angustifolia* has a higher adaptive ability to acclimate to flooding and shade stresses than does *P. australis*, which might be an important reason for their different distribution patterns.

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Introduction

The Sanjiang Plain (45°01' ~ 48°28'N, 130°13' ~ 135°05'E) is the largest freshwater marsh in China, about 108,900 km² (Luo and Xie 2009). In the plain, one of the dominant species *Deyeuxia angustifolia* usually distributes widely in typical meadow or marsh and occupies an area of about 1.24×10^4 km², while *Phragmites australis*, the concomitant species, is

distributed sparsely in the *D. angustifolia* communities or relative open sites with an area of about $8.87 \times 10^2 \text{ km}^2$ (Yi et al. 1985; Li et al. 2009). To date, little is known about the mechanisms controlling their distributional patterns.

Flooding is the predominant factor determining plant growth and distribution in wetland ecosystems mainly due to the reduced oxygen availability and redox potential (Eh) in the soil (Van Eck et al. 2006; Iwanaga and Yamamoto 2008; Luo and Xie 2009). Tolerance to flooding varies among species, which can be reflected by the distribution of species along water-level gradients. For flood-tolerant plants, adaptive characteristics include the changes of shoot: root ratios, elongation of stem, development of intercellular spaces in lenticels, formation of aerenchyma and adventitious roots, as well as shallow root systems (Iwanaga and Yamamoto 2008; Xie et al. 2008; Luo and Xie 2009). These morphological changes allow plants to acclimate to anaerobic conditions by increasing oxygen transport to roots or by reducing radial oxygen loss to the soil (Blom and Voesenek 1996; Luo and Xie. 2009).

Light is another limiting factor influencing plant survival and growth in wetlands, especially for seedlings (Krauss and Allen 2003; Going et al. 2008). For example, in *D. angustifolia* communities of Sanjiang Plain, thick litter layer (up to 20–30 cm) could decrease the radiation amount and light quality significantly, consequently inhibit seed germination and seedling establishment (Li et al. 2009). To survive in low light conditions, seedling usually adjusts their morphology, such as decreasing leaf thickness and increasing leaf area, shoot: root ratio and stem height, to increase their opportunities to exposure to ambient light (Kennedy et al. 2007; Going et al. 2008). Therefore, the different response of morphological plasticity among species might reflect their abilities to occupy habitats in the nature (Ryser and Eek 2000).

Moreover, plant growth is usually affected by flooding and shading simultaneously, which makes it difficult to predict plant distribution patterns on the basis of single factor (Chapin et al. 1987; Lenssen et al. 2003). Higher water level might facilitate (Mommer et al. 2005) or inhibit (Geiger and Servaites 1991; Lenssen et al. 2003) plant to acclimate to shade, then leading to the interactive effect differently with the expected influence on the basis of both separate

effects. Furthermore, Lenssen et al. (2003) found that interactive effects existed in flood-sensitive species rather than flood-tolerant plants. Although many studies have been conducted on the effect of water level and light on plant performance, respectively (Xu et al. 2005; Van Eck et al. 2006; Iwanaga and Yamamoto 2008), the combined effects and their potential interactions in determining plant distributions are poorly understood (Mommer et al. 2005; Battaglia and Sharitz 2006).

Here we want to identify the role of water level, light and their potential interactions on the different distributions between *D. angustifolia* and *P. australis* in the Sanjiang Plain. To this end, seedlings of *D. angustifolia* and *P. australis* were treated with three irradiances and two water levels under greenhouse conditions and their growth performance and biomass allocation pattern were investigated to test the following hypothesis: (1) both high water level and shade have a more profoundly negative effect on the growth of *P. australis* than that of *D. angustifolia*, since the later as a dominant species should be more tolerant to stressful environments; (2) the adaptive strategies (such as biomass allocation, stem elongation) to acclimate to higher water level and shade are more effective in *D. angustifolia* than in *P. australis*, since the former as a dominant species should be a successful competitor to occupy habitat at higher water level and lower irradiance.

Materials and methods

Plant material

The seeds of both species were collected in August, 2006 from the Sanjiang Mire Wetland Experimental Station (47°35'N, 133°31'E), the Chinese Academy of Sciences, in the eastern part of Heilongjiang Province, China. The station is permanently inundated and referred to as eutrophic freshwater marsh. The average elevation is 56 m above sea level. The mean annual precipitation is 600 mm and the mean temperature was 1.9°C. The water and soil in marshes are completely frozen from October to April and begin to melt from late April to July (Ding et al. 2002). Prior to the experiment, the seeds were rinsed with distilled water, and then sterilized with potassium permanganate solution (0.1%) for 10 min,

followed by a second rinse with distilled water, and finally soaked in distilled water for 24 h. Seeds were germinated in November 19, 2006 in 150 plastic bottles (1.5 L, 16 cm in height) for each species. Prior to sowing, each bottle was filled with 6-cm soil collected from the Sanjiang Freshwater Marsh Field Observation Station (31 g kg⁻¹ organic matter, 155 mg kg⁻¹ exchangeable N and 13.4 mg kg⁻¹ exchangeable P). After that, 10 seeds of *D. angustifolia* were planted in each bottle, but 30 seeds of *P. australis* were planted per bottle due to low germination rates (Li et al. 2009). The temperature was kept at 25 ± 2°C during the day and 15 ± 2°C at night, and the light was provided by 400 watt sodium lamps at a photon flux density of 300 μmol m⁻² s⁻¹ (PAR) in a 14-h photoperiod. Tap water (containing 51.1 μg l⁻¹ NH₄⁺-N, 176 μg l⁻¹ NO₃⁻-N and 52.7 μg l⁻¹ PO₄³⁺-P, pH = 7.2) was supplied daily according to the plant growth. After 14 days, only one seedling (size 7–8 cm in height) was left in each bottle.

Experimental design and harvest

A two-way factorial design was used in the experiment, which consisted of three irradiances (300, 100, 20 μmol m⁻² s⁻¹) and two water levels (0 and 5 cm, relative to soil surface). The lowest light irradiance was chosen based on another experiment, which found that both the seedlings of *P. australis* and *D. angustifolia* can survive under 20 μmol m⁻² s⁻¹ (Li et al. 2009). The water depth was chosen based on the work of Ding et al. (2002) who found that the standing water depth ranged from 0 to 5 cm in *D. angustifolia* marshes in this area. Prior to the experiment, growth parameters (biomass, height) of five seedlings for each species were measured. A total of 120 seedlings per species were chosen for the experiment. Therefore, 120 bottles (one seedling per bottle) were used for each treatment of each species. Light reduction was obtained by different layers of nylon-nets. Tap water was supplied daily to maintain the water level.

Plants were harvested at 7, 14, 21 and 28 days after the start of the experiment, respectively. For each harvest, five seedlings of each treatment were dug out, and care was taken to collect all the roots. Roots were cleaned with tap water. Plant height was measured, then the plants were divided into leaves,

roots and stems, dried at 80°C for 48 h and weighed for biomass evaluation.

Calculation and data analysis

Plant biomass was the sum of each tissue mass. In order to perform functional growth analysis on biomass allocation to correct for size differences among plants, adjusted allometric analysis (biomass fractions in allocation) suggested by Poorter and Nagel (2000) was applied. Leaf mass fraction, stem mass fraction and root mass fraction were calculated as the ratio of leaf mass, stem mass and root mass to the plant biomass. Relative growth rate (RGR) and relative elongation rate (RER) were determined as: $RGR = (\ln w_2 - \ln w_1) / (t_2 - t_1)$, $RER = (\ln h_2 - \ln h_1) / (t_2 - t_1)$, where w_1 was the initial biomass, w_2 the biomass at harvest time t_2 , h_1 the initial plant height, h_2 the plant height at harvest time t_2 and $(t_2 - t_1)$ the experimental time.

Repeated-measures ANOVAs, using water level and light irradiance as dependent factors and harvest time as repeated-measures factor, were used to evaluate treatment effects on biomass, RGR, height, RER, leaf mass fraction, stem mass fraction and root mass fraction of the two species. Prior to analysis, sphericity was tested using Mauchly's test. Data were log₁₀-transformed, if necessary, to reduce heterogeneity of variances and normality and homogeneity were tested using Liljefer's test and Levene's test, respectively. Multiple comparisons of means were performed by Duncan's test at 0.05 significance level.

Results

Biomass accumulation and mean relative growth rate (RGR)

Biomass accumulation of *D. angustifolia* was significantly reduced by the reduction of light availability alone ($P < 0.001$; Table 1). At the end of the experiment, biomass accumulation of *D. angustifolia* at high irradiance (149.12–154.70 mg per plant; Table 2) was 24.2–27.0 times higher than at low irradiance (6.12–5.72 mg per plant; Table 2). Biomass accumulation of *P. australis* decreased significantly in accord with the reduction of light availability ($P < 0.001$; Table 1) and enhancement of water level ($P < 0.001$; Tables 1, 2). Moreover, light

Table 1 Summary of repeated-measures ANOVAs for the growth of *Deyeuxia angustifolia* and *Phragmites australis* seedlings under three light irradiances and two water levels (*F*-values)

| Parameter | Species | <i>n</i> | Light (<i>L</i>) | Water level (<i>W</i>) | <i>L</i> × <i>W</i> |
|---|------------------------|----------|---------------------|--------------------------|---------------------|
| Biomass (g) | <i>D. angustifolia</i> | 5 | 80.784*** | 0.190 ^{NS} | 0.039 ^{NS} |
| | <i>P. australis</i> | 5 | 119.762*** | 37.757*** | 12.525*** |
| Relative growth rate (g g ⁻¹ day ⁻¹) | <i>D. angustifolia</i> | 5 | 103.193*** | 2.197 ^{NS} | 1.122 ^{NS} |
| | <i>P. australis</i> | 5 | 53.768*** | 24.690*** | 1.217 ^{NS} |
| Height (cm) | <i>D. angustifolia</i> | 5 | 80.459*** | 1.537 ^{NS} | 0.092 ^{NS} |
| | <i>P. australis</i> | 5 | 353.482*** | 60.166*** | 12.403*** |
| Relative elongation rate (cm cm ⁻¹ day ⁻¹) | <i>D. angustifolia</i> | 5 | 26.296*** | 0.027 ^{NS} | 1.147 ^{NS} |
| | <i>P. australis</i> | 5 | 36.112*** | 6.187* | 1.227 ^{NS} |
| Leaf mass fraction | <i>D. angustifolia</i> | 5 | 2.202 ^{NS} | 4.557* | 6.717** |
| | <i>P. australis</i> | 5 | 97.586*** | 20.001*** | 71.357*** |
| Root mass fraction | <i>D. angustifolia</i> | 5 | 19.280*** | 3.543 ^{NS} | 11.273*** |
| | <i>P. australis</i> | 5 | 61.112*** | 34.388*** | 18.095*** |
| Stem mass fraction | <i>D. angustifolia</i> | 5 | 55.870*** | 48.408*** | 5.472* |
| | <i>P. australis</i> | 5 | 271.311*** | 0.757 ^{NS} | 64.709*** |

^{NS} *P* > 0.05; * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001

Table 2 Biomass accumulation (Mean ± SE, *N* = 5) of *Deyeuxia angustifolia* and *Phragmites australis* seedlings growing in three light irradiances and two water levels

| Days | Species | Biomass of treatments (mg) | | | | | |
|------|------------------------|------------------------------|-----------------------------|---------------------------|-----------------------------|--------------------------|----------------------------|
| | | HL and HW | HL and LW | ML and HW | ML and LW | LL and HW | LL and LW |
| 7 | <i>D. angustifolia</i> | 14.66 ± 3.97 ^a | 11.82 ± 1.43 ^{ab} | 5.02 ± 1.15 ^{bc} | 2.54 ± 0.29 ^c | 4.00 ± 0.73 ^c | 3.70 ± 0.51 ^c |
| | <i>P. australis</i> | 11.58 ± 1.42 ^b | 31.32 ± 5.24 ^a | 6.46 ± 1.00 ^b | 9.44 ± 1.55 ^b | 7.16 ± 2.20 ^b | 9.28 ± 1.36 ^b |
| 14 | <i>D. angustifolia</i> | 26.28 ± 4.36 ^a | 21.80 ± 2.52 ^a | 10.68 ± 3.97 ^b | 6.22 ± 0.91 ^b | 2.20 ± 0.32 ^c | 2.98 ± 0.72 ^c |
| | <i>P. australis</i> | 30.78 ± 8.47 ^b | 112.72 ± 14.47 ^a | 7.26 ± 1.47 ^c | 17.76 ± 4.25 ^b | 6.38 ± 1.52 ^c | 8.34 ± 1.27 ^c |
| 21 | <i>D. angustifolia</i> | 73.86 ± 15.22 ^a | 90.78 ± 17.56 ^a | 19.22 ± 2.24 ^b | 16.14 ± 4.32 ^b | 2.44 ± 0.37 ^c | 3.20 ± 0.70 ^c |
| | <i>P. australis</i> | 90.16 ± 11.56 ^b | 185.76 ± 21.58 ^a | 14.64 ± 1.72 ^c | 62.38 ± 9.72 ^b | 7.44 ± 1.54 ^d | 12.98 ± 3.19 ^{cd} |
| 28 | <i>D. angustifolia</i> | 149.12 ± 32.72 ^a | 154.70 ± 11.22 ^a | 17.68 ± 0.28 ^b | 38.06 ± 8.01 ^b | 6.12 ± 1.11 ^c | 5.72 ± 0.29 ^c |
| | <i>P. australis</i> | 211.60 ± 25.40 ^{ab} | 355.72 ± 69.63 ^a | 26.60 ± 2.62 ^c | 104.44 ± 19.63 ^b | 7.70 ± 1.36 ^d | 13.10 ± 1.44 ^{cd} |

Different letters indicate significant difference among treatments at the 0.05 significance level. HL and HW, HL and LW, ML and HW, ML and LW, LL and HW, LL and LW means high light and high water level, high light and low water level, medium light and high water level, medium light and low water level, low light and high water level, low light and low water level treatments, respectively

and water level had a combined negative effect on biomass accumulation of *P. australis* at medium and high irradiance (*P* < 0.001; Table 1).

RGRs were similar to biomass accumulation, and decreased significantly with the reduction of light availability in both *P. australis* (*P* < 0.001; Table 1) and *D. angustifolia* (*P* < 0.001; Table 1). At the end of experiment, RGR of *D. angustifolia* at high

irradiance (0.120–0.126 g g⁻¹ day⁻¹; Fig. 1) was 14.2–15.0 times higher than that at low irradiance (0.008–0.009 g g⁻¹ day⁻¹; Fig. 1). At 5-cm water level, RGR of *P. australis* was 15.2 times higher at high irradiance (0.128 g g⁻¹ day⁻¹; Fig. 1) than at low irradiance (0.008 g g⁻¹ day⁻¹; Fig. 1), while at 0-cm water level, RGR of *P. australis* at high irradiance was only 5 times higher than that at low

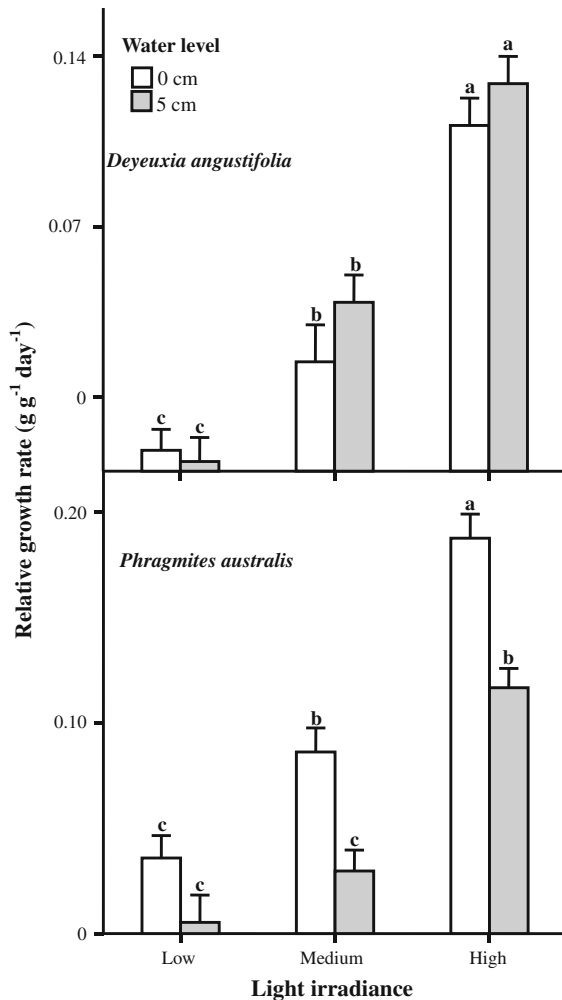


Fig. 1 Mean relative growth rate (Mean \pm SE, $N = 5$) of *Deyeuxia angustifolia* and *Phragmites australis* seedlings growing in three light irradiances and two water levels. Different letters indicate significant difference among treatments at the 0.05 significance level

irradiance. Higher water level led to a lower RGR in *P. australis* ($P < 0.001$; Table 1; Fig. 1), but had insignificant effect in *D. angustifolia* ($P > 0.05$; Table 1; Fig. 1).

Plant height and mean relative elongation rate (RER)

The height of *P. australis* was significantly affected by both light ($P < 0.001$; Table 1) and water level ($P < 0.001$; Table 1), with significant interactions ($P < 0.001$; Table 1). Plants were highest at high irradiance + 0 cm water level (53.2 cm per plant,

28 days; Table 3) and shortest at low irradiance + 5 cm water level (10.5 cm per plant, 28 days; Table 3). Moreover, significant effect of water level was only found at medium and high irradiance (Table 3). The height of *D. angustifolia* was only affected by light ($P < 0.001$; Table 1), rather than by water level ($P > 0.05$; Table 1). At the end of the experiment, the height of *D. angustifolia* at high irradiance (40.3–45.0 cm per plant; Table 3) was about 1.95 times higher than that at low irradiance (20.8–22.8 cm per plant; Table 3).

RER decreased significantly with the reduction of light availability in both *D. angustifolia* ($P < 0.001$; Table 1) and *P. australis* ($P < 0.001$; Table 1). From high to low irradiance, RER decreased 57.6–75.6% in *D. angustifolia* but 78.0–80.8% in the seedlings of *P. australis* (Fig. 2). RER of *D. angustifolia* seedlings at low irradiance (0.016–0.023 cm cm⁻¹ day⁻¹; Fig. 2) was higher than that of *P. australis* (0.014–0.018 cm cm⁻¹ day⁻¹; Fig. 2). However, RER of *D. angustifolia* at high irradiance (0.054–0.064 cm cm⁻¹ day⁻¹; Fig. 2) was lower than that of *P. australis* (0.065–0.091 cm cm⁻¹ day⁻¹; Fig. 2). RER of *P. australis* was also significantly affected by water level ($P < 0.05$; Table 1). At medium and high irradiance, RER at 0-cm water level (0.053–0.091 cm cm⁻¹ day⁻¹; Fig. 2) was about 1.4 times higher than that at 5-cm water level (0.037–0.065 cm cm⁻¹ day⁻¹; Fig. 2). However, water level had no effect on the RER of *D. angustifolia* ($P > 0.05$; Table 1).

Biomass allocation

Biomass allocation of both species were significantly affected by light availability ($P < 0.001$; Table 1; Fig. 3), except for the leaf mass fraction of *D. angustifolia* ($P > 0.05$; Table 1; Fig. 3). The root mass fraction of *D. angustifolia* at 5-cm water level significantly decreased with the reduction of light availability. However, opposite result was found in *P. australis* seedlings. Seedlings of *D. angustifolia* had a higher stem mass fraction at low and medium irradiance than that at high irradiance, while the stem mass fraction of *P. australis* was highest at high irradiance. Water level had a significant influence on the biomass allocation of both species ($P < 0.001$; Table 1; Fig. 3), except for the root mass fraction of *D. angustifolia* ($P > 0.05$; Table 1; Fig. 3) and the stem mass fraction of *P. australis* ($P > 0.05$; Table 1;

Table 3 Height (Mean \pm SE, $N = 5$) of *Deyeuxia angustifolia* and *Phragmites australis* seedlings growing in three light irradiances and two water levels

| Days | Species | Height of treatments (cm) | | | | | |
|------|------------------------|--------------------------------|-------------------------------|-------------------------------|--------------------------------|-------------------------------|-------------------------------|
| | | HL and HW | HL and LW | ML and HW | ML and LW | LL and HW | LL and LW |
| 7 | <i>D. angustifolia</i> | 18.02 \pm 2.09 ^a | 12.54 \pm 1.07 ^a | 13.82 \pm 1.88 ^a | 12.96 \pm 0.63 ^a | 13.90 \pm 1.20 ^a | 14.22 \pm 2.26 ^a |
| | <i>P. australis</i> | 13.50 \pm 1.05 ^{ab} | 19.50 \pm 2.44 ^a | 11.26 \pm 1.64 ^b | 11.24 \pm 1.60 ^b | 10.16 \pm 1.81 ^b | 10.40 \pm 1.13 ^b |
| 14 | <i>D. angustifolia</i> | 23.46 \pm 2.09 ^a | 24.96 \pm 2.18 ^a | 23.72 \pm 3.89 ^a | 21.68 \pm 1.78 ^a | 8.18 \pm 0.74 ^b | 11.20 \pm 1.84 ^b |
| | <i>P. australis</i> | 20.64 \pm 3.07 ^b | 37.04 \pm 2.21 ^a | 11.48 \pm 1.02 ^c | 18.02 \pm 2.46 ^{bc} | 10.66 \pm 1.06 ^c | 10.16 \pm 1.05 ^c |
| 21 | <i>D. angustifolia</i> | 38.50 \pm 1.79 ^{ab} | 40.48 \pm 3.31 ^a | 31.40 \pm 2.14 ^b | 32.06 \pm 4.24 ^b | 12.52 \pm 1.41 ^c | 13.50 \pm 1.87 ^c |
| | <i>P. australis</i> | 37.40 \pm 1.66 ^{ab} | 42.24 \pm 1.33 ^a | 21.50 \pm 1.79 ^c | 33.60 \pm 3.39 ^b | 11.44 \pm 1.10 ^d | 12.10 \pm 1.19 ^d |
| 28 | <i>D. angustifolia</i> | 40.30 \pm 2.55 ^{ab} | 45.00 \pm 1.87 ^a | 34.40 \pm 3.53 ^b | 43.40 \pm 1.57 ^{ab} | 20.80 \pm 1.78 ^c | 22.80 \pm 1.24 ^c |
| | <i>P. australis</i> | 46.10 \pm 2.23 ^b | 53.20 \pm 4.14 ^a | 31.90 \pm 1.76 ^c | 41.60 \pm 2.62 ^b | 10.50 \pm 0.88 ^d | 12.40 \pm 1.41 ^d |

Different letters indicate significant difference among treatments at the 0.05 significance level. HL and HW, HL and LW, ML and HW, ML and LW, LL and HW, LL and LW means high light and high water level, high light and low water level, medium light and high water level, medium light and low water level, low light and high water level, low light and low water level treatments, respectively

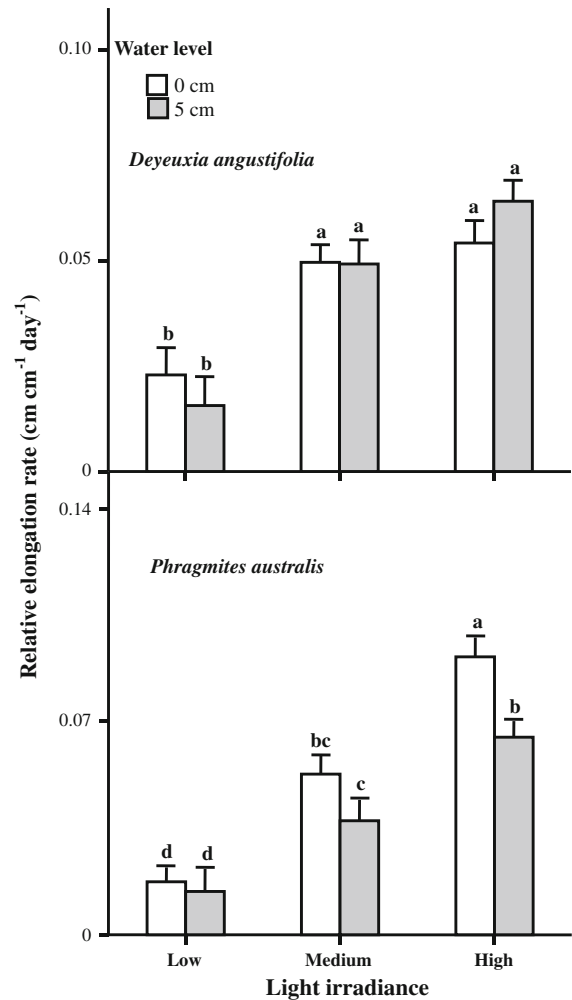


Fig. 2 Mean relative elongation rate (Mean \pm SE, $N = 5$) of *Deyeuxia angustifolia* and *Phragmites australis* seedlings growing in three light irradiances and two water levels. Different letters indicate significant difference among treatments at the 0.05 significance level

Fig. 3). At low irradiance, the root mass fraction of *P. australis* at 5-cm water level was higher than that at 0-cm water level. The stem mass fraction of *D. angustifolia* was higher at 0-cm than at 5-cm water level.

Discussion

Seedling phase is the most crucial and sensitive stage in the plant life history (Peterson and Baldwin 2004). Many environmental factors, such as light, flooding, competition and nutrients may act as an

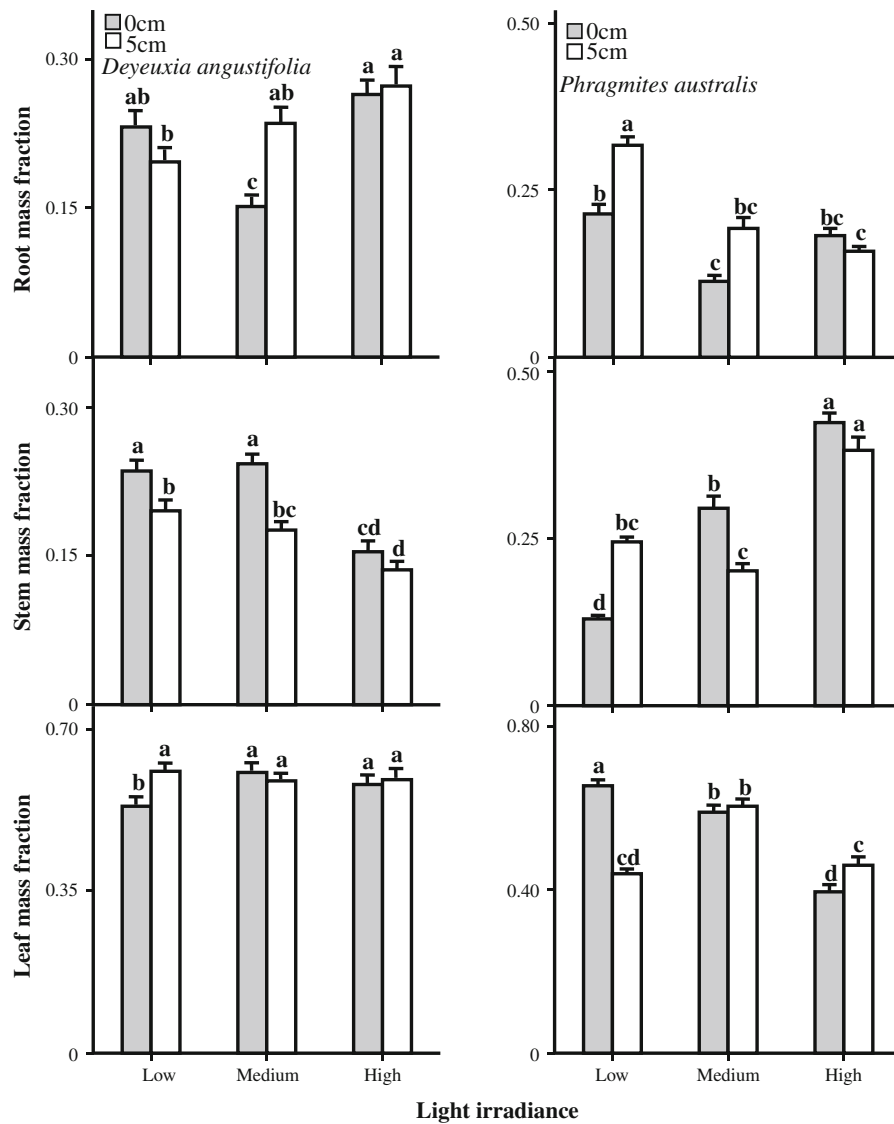


Fig. 3 Biomass allocation patterns of (Mean ± SE, N = 5) *Deyeuxia angustifolia* and *Phragmites australis* seedlings growing in three light irradiances and two water levels. Different letters indicate significant difference among treatments at the 0.05 significance level

environmental sieve influencing the recruitment of new seedlings, and determining plant distribution to a certain degree. Our study confirmed that light significantly decreases biomass, RGR, height and RER of both *D. angustifolia* and *P. australis*, which suggests that light plays an important role in determining plant distributions in the Sanjiang Plain. Furthermore, biomass allocation of both species were also influenced by light limitation except for the leaf mass fraction of *D. angustifolia*. Higher stem mass fraction in *D. angustifolia* at low irradiance indicated that

more energy was allocated to the stem to facilitate its elongation, which is a useful strategy for plant to grow out of the shade and to grow more emergent leaves for photosynthesis (Wang et al. 2008). However, the stem mass fraction of *P. australis* decreased significantly with the reduction of irradiance, suggesting that it could not resist shade stress by stem elongation. Moreover, higher RER of *D. angustifolia* at low irradiance suggested that *D. angustifolia* had a higher ability to escape from shade stresses than that of *P. australis*. Our result is also supported by another

study (Li et al. 2009), which showed that the survival rate of *D. angustifolia* at low irradiance was higher than that of *P. australis* due to higher leaf morphological plasticity.

The growth responses to water level were species-specific. Enhancement of stem mass fraction and RER are important adaptive strategies for plant to acclimate to flooding stress (Laan and Blom 1990). In this experiment, biomass accumulation, RGR, height and RER of *P. australis* were significantly inhibited by higher water level. However, water level had no effects on the growth of *D. angustifolia*. These results indicated that *D. angustifolia* could grow better than *P. australis* at 5-cm water level. For *P. australis*, the negative effects of flooding on plant growth were also found in other studies (Blanch et al. 1999; Edwards et al. 2003), due to poor soil aeration and depletion of oxygen in the rhizosphere of plants (Xie et al. 2008). Moreover, Deegan et al. (2007) also confirmed that the below-ground parts of *P. australis* usually had low aeration efficiency. However, the stem mass fraction of *P. australis* was not affected by water level and RER was lower at 5-cm water level. This result is contrary to the study of Vretare et al. (2001), which showed that *P. australis* could allocate more energy to the above-ground part to increase the stem height when treated with 70–75 cm water depth. The response of plants to the same environmental stress might be different with life stage or stress intensities (Battaglia et al. 2000). Stem mass fraction of *D. angustifolia* at 5-cm water level was lower than that at 0-cm water level, indicating that enhancement of stem mass fraction was not the effective strategy for *D. angustifolia* to acclimate to flooding. Study by Xie et al. (2008) confirmed that *D. angustifolia* could resist flooding stress mainly by the positive adjustment of root growth, such as shallow root systems and increased root porosity.

When plants were stressed with flooding and shade simultaneously, their growths were not only influenced by these two factors, respectively, but also by their interactions. Generally, three modes of interactions could be occurred: (1) amplified effect, which means that the adjustment of plant to acclimate to shade would be prevent by higher water level, then lead to the total effect on flooded, shaded plants is stronger than expected on the basis of both separate effects (Lenssen et al. 2003); (2) independently effect, no interactions could be found in this case; (3) reduced

effect, which could be occurred in the case that one stress is so strong that additional limitations hardly depress plant growth any further (Chapin et al. 1987; Urbas and Zoble 2000; Lenssen et al. 2003). In our experiment, interactions were found in *P. australis*, for the influence of water level changed greatly under different light conditions. At low irradiance, similar growth performance between two water levels indicated that the negative effect of shade was so strong that making water level hardly inhibit *P. australis* growth any more. Reduced effect was also found in some other studies, but in contrast to our study, these studies confirmed that higher water level was the stronger limitation on plant growth than shade (Dale and Causton 1992; Lenssen et al. 2003). One possible reason for the difference is that the water level in our study was so shallow (only 5 cm) that resulting its negative effect was smaller than shading. However, interactions had insignificant effect on the growth of *D. angustifolia*, mainly because the growth was not affected by water level and these differences confirmed that *D. angustifolia* had a higher adaptive abilities than did *P. australis* to acclimate to the simultaneous stresses of flooding and shade, which might be an important reason accounting for their different distribution patterns in the Sanjiang Plain.

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