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Research

Morphological responses of two plant species from different elevations in the Dongting Lake wetlands, China, to variation in water levels

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The vegetation of wetlands show strong zonation patterns, but the mechanisms determining these patterns are not fully understood. In the present study, growth and morphological responses to a water level gradient (–20 cm (i.e. water level 20 cm below soil surface), –10 cm, 0 cm, 10 cm, 20 cm) were compared between a higher elevation plant (*Imperata cylindrica*) and a lower elevation plant (*Carex brevicuspis*) in the Dongting Lake wetlands of China. For both species, the aboveground, belowground, and total biomass were greater at –10 cm than at any other water level.. However, when the water level increased from –10 cm to 0 cm, there was a greater decrease in the biomass of *I. cylindrica* than in that of *C. brevicuspis*. Plant height, tiller number, leaf length, leaf width and leaf area showed greater variation along the water level gradient in *I. cylindrica* than in *C. brevicuspis*. Generally, with increasing water level, root length, rhizome number, and adventitious root biomass and number all decreased in *I. cylindrica*. However, in *C. brevicuspis*, neither the rhizome number nor the primary adventitious root biomass differed significantly among the five water levels. These results indicate that *I. cylindrica* have a lower tolerance for flooding and higher water sensitivity than *C. brevicuspis* and these differences may explain why *I. cylindrica* is found at relatively higher elevations that are not prone to flooding, while *C. brevicuspis* is found at comparatively lower elevations in the Dongting Lake wetlands.

Keywords: *Imperata cylindrical*, *Carex brevicuspis*, flooding, drought, water tolerance, water sensitivity

Introduction

Wetland vegetation is characterized by distinct zonation patterns (Pennings et al. 2005, Sadro et al. 2007, Chen et al. 2015). Depending on their habitat, plants may be classified as submerged, floating-leaved, emergent, mesophytic or xerophytic (Vis et al. 2003, Dahlgren and Ehrlén 2005). Submerged and floating-leaved plants are mainly found in water and damp mud but only rarely on dry land. In contrast, mesophytic and xerophytic plants are usually found on dry land and only occasionally in water. Emergent plants have a lower tolerance for flooding than submerged plants and lower tolerance of drought than mesophytes.

Several studies have investigated the various factors affecting plant zonation patterns (Riis et al. 2001, Dahlgren and Ehrlén 2005, Sadro et al. 2007). Meteorological, hydrological, edaphic, and biotic factors can all affect plant distribution (Sadro et al. 2007, Wilcox and Nichols 2008, Chen et al. 2015). In wetland ecosystems, the hydrological regime is the most important governing factor that affects plant growth (Hsiao 1973, Bendix and Hupp 2000, Visser et al. 2003, Li et al. 2011a, Dawood et al. 2016, Ding et al. 2017). Flooding and drought generally inhibit plant photosynthesis and decrease biomass accumulation (Mishra et al. 2008, Arbona et al. 2009, Ding et al. 2017). To alleviate the effects of excess water and in order to increase access to light and oxygen, plants increase aboveground biomass allocation by stem elongation (Visser et al. 2003, Jackson 2008). Conversely, during drought, plants may increase underground biomass allocation by elongating roots that increase water uptake (Iwanaga and Yamamoto 2008, Li et al. 2011b). However, the degree of water stress for any given water condition varies by plant species. For example, when the water level dropped from 0 cm to –25 cm, *Miscanthus sacchariflorus*, a high-elevation plant, showed a greater drought tolerance and maintained a higher growth rate than *Polygonum hydropiper*, a low-elevation plant (Li et al. 2013). Therefore, species specific plant growth and morphological responses to water level changes may reflect their natural distribution. Flooding-tolerant species are generally distributed in low-elevation areas, whereas drought-tolerant species are found in high-elevation zones (Luo et al. 2008, Chen et al. 2015).

With its 2625 km^2, Dongting Lake (28°38′–29°45′N, 111°40′–113°10′E) is the second largest freshwater lake in China at. The plant communities on the shores show obvious zonation patterns (Li et al. 2013, Chen et al. 2015) and the diversity of mesophytic and emergent plants decrease with increasing water level, whereas that of floating-leaved and submerged plants increase (Xie and Chen 2008). However, the mechanisms influencing these zonation patterns are poorly understood. Therefore, models designed to predict plant species dynamics and succession in wetlands are not backed by adequate scientific evidence. In the present study, an experiment was conducted using plants from the Dongting Lakes wetlands involving a higher elevation plant (*Imperata cylindrica*) and a lower elevation plant (*Carex brevicuspis*). The objective was to examine the relationship between the natural distribution of these species and their morphological responses to five different water levels (–20 cm, –10 cm, 0 cm, 10 cm and 20 cm).

Material and methods

Plant material and study area

Dongting Lake is fed by annual floodwaters from the Yangtze, Xiang, Zi, Yuan and Li Rivers. The lake catchment has a subtropical monsoon climate with an average annual temperature of 17°C, an average wind speed of 2.5 m s^{-1}, and 268 frost-free days. The mean annual precipitation ranges from 1200 mm to 1415 mm. The rainy season extends from April to August and the flooding period from May to October. The average relative humidity is 80% and the average evaporation is 1270 mm (Xie et al. 2015). Elevation at the soil surface ranges from 28 m to 35 m a.s.l

In early May 2015, 200 seedlings of *Imperata cylindrica* and *Carex brevicuspis* were collected from the East Dongting Lake wetlands. *Imperata cylindrica* is a perennial mesophytic plant, growing on a relatively high elevation (33 m a.s.l.) bank of the lake that is not submerged during the flooding season. *Carex brevicuspis* is a perennial emergent species, which occupies a low-elevation (30 m a.s.l.) bank at the lake and is submerged during the flooding period. They were transplanted to an outdoor nursery at the Dongting Lake Station for Wetland Ecosystem Research, CAS (29°29′59.12″N, 112°47′51.56″E). In early July, each seedling was transplanted into a PVC tube (11 cm diameter; 25 cm height) fitted with plastic mesh on the bottom to allow for drainage. Each tube was filled with 24 cm well-mixed soil collected from a medium-elevation (32 m a.s.l.) bank of the East Dongting Lake wetlands (organic matter: 28 g kg^{-1}, using the $K_2Cr_2O_7$-H_2SO_4 oxidation method; total N: 1.7 g kg^{-1}, using the micro-Kjeldahl method; total P: 1.5 g kg^{-1}, using the ascorbic acid reduction method after samples were digested with NaOH). The tubes were placed in outdoor plastic drums (98 cm length, 76 cm width, 68 cm height) and the water level in the drums relative to the soil surface was maintained at 0 cm by replenishing with tap water (51.1 μg l^{-1} NH_4-N, 176 μg l^{-1} NO_3-N, 52.7 μg l^{-1} PO_4^{3+}-P, pH = 7.2).

Experimental design

On day 10 after transplantation, 60 seedlings of each species with approximately equal height (21 cm for *C. brevicuspis*, 46 cm for *I. cylindrica*), leaf number (5 for *C. brevicuspis*, 6 for *I. cylindrica*), dry biomass (1.0 g for *C. brevicuspis*, 8.8 g for *I. cylindrica*) were selected for the water level treatments. A two-way factorial design was used for this experiment. It consisted of the two plant species (*I. cylindrica* and *C. brevicuspis*) and five water levels (–20 cm: water level 20 cm below soil surface; –10 cm: water level 10 cm below soil surface; 0 cm: water level at soil surface; 10 cm: water level 10 cm above soil surface; and 20 cm: water level 20 cm above soil surface). Six plastic drums were prepared for the experiment and placed on flat ground with natural light and temperature. Each drum contained both plant species and five water

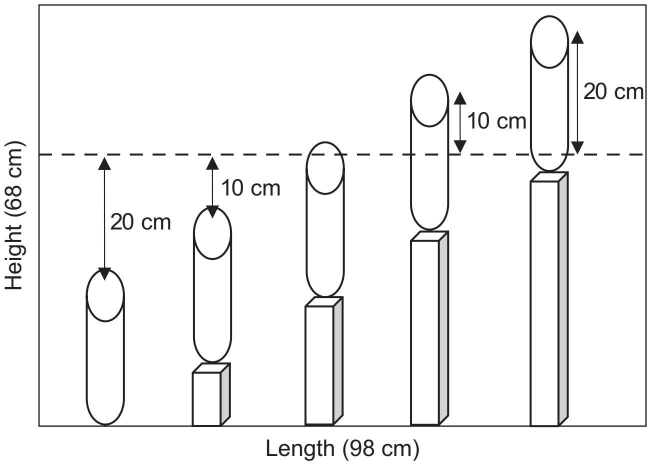

Figure 1. Height of PVC tubes containing *Imperata cylindrica* and *Carex brevicuspis* seedlings in plastic drums. The dotted line represents the water level. The cylinders represent the PVC tubes and the cuboids are bricks. Five treatments were used: –20 cm water level (water level 20 cm below soil surface); –10 cm water level (water level 10 cm below soil surface); 0 cm water level (water level at soil surface); 10 cm water level (water level 10 cm above soil surface); 20 cm water level (water level 20 cm above soil surface).

levels (Fig. 1). A total of 120 seedlings were used and there were 20 seedlings per drum. Tap water was regularly added to maintain the water level.

Plant harvest

The immature plants were harvested on day 110 of the experimental treatment. Plants from each treatment were excavated and any soil adhering to the roots was removed. The roots were rinsed with tap water. The tiller, leaves, rhizome and primary adventitious roots were counted. Shoot height and root length were measured. Leaf length, width and area were measured using a portable area meter. Shoots and roots were then separated and dried at 80°C for 48 h to constant weight.

Data analysis

Multiple comparisons were made among plant biomass (aboveground, underground and total) and morphological characteristics (shoot height, no. of tillers, no. of leaves, leaf length, leaf width, leaf area, root length, no. of rhizomes, primary adventitious root biomass and no. of primary adventitious roots) for the two plant species and five water levels. Tukey's test was used at a significance level of 0.05. Prior to the analysis, Levene's test was run to determine the homogeneity of the variances. Data were $\log_{10}$-transformed where necessary to reduce variance heterogeneity. All statistical analyses were performed in SPSS ver. 18.0 (IBM Corp.).

Results

Plant biomass

Plant biomass significantly differed among the five water levels (Fig. 2). For *Imperata cylindrica*, the ascending order for all three types of biomass (aboveground, underground and total)

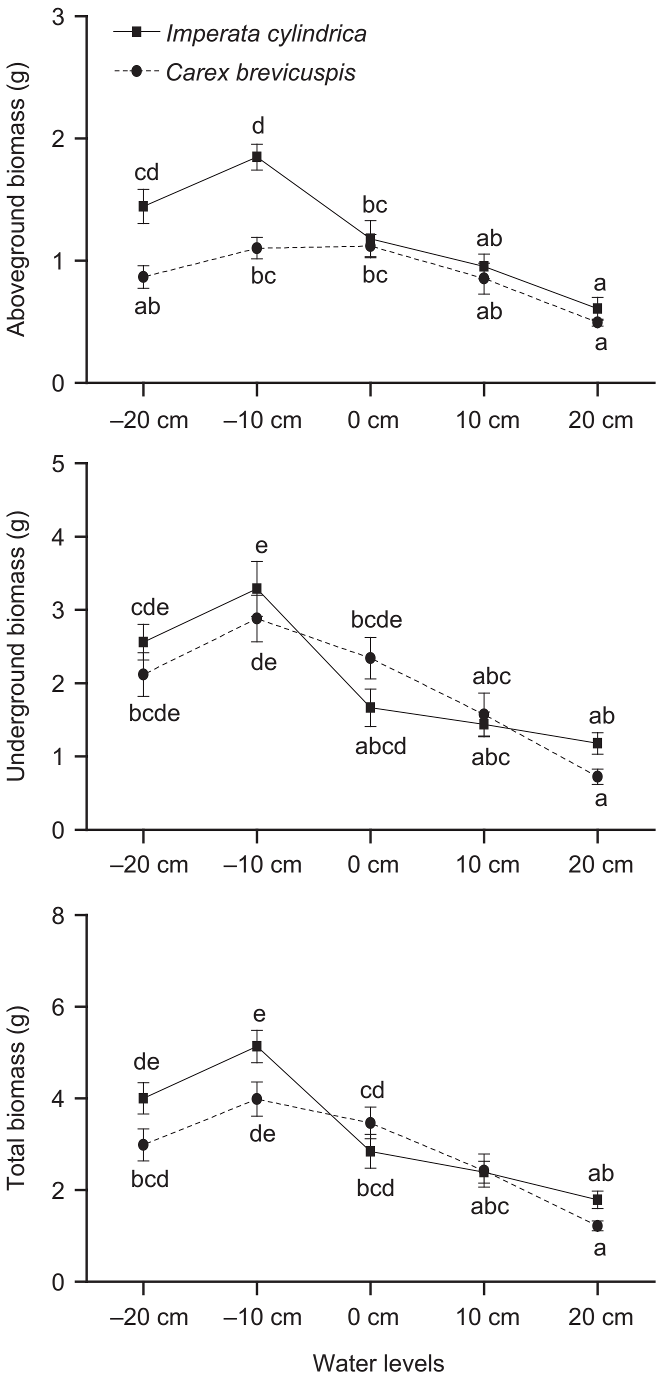

Figure 2. Plant biomass (means ± SE) of two species (*Imperata cylindrica* and *Carex brevicuspis*) grown at five different water levels. Means not sharing a common letter differ significantly among treatments at $p < 0.05$ based on Tukey's test.

was 20 cm ≤ 10 cm ≤ 0 cm ≤ –20 cm ≤ –10 cm. In contrast, for *Carex brevicuspis* the three types of biomass showed different patterns with variation in water level (Fig. 2). For example, the aboveground biomass was lowest at 20 cm, intermediate at 10 cm and –20 cm, and highest at 0 cm and –10 cm, while the underground and total biomasses were lowest at 20 cm, intermediate at 10 cm, –20 cm and 0 cm, and highest at –10 cm.

Aboveground morphology

For *I. cylindrica*, plant height on day 110 ranged from 50.9 cm to 80.0 cm and tiller number from 2.3 to 7.3 for the five water level treatments. These two parameters were significantly higher at the –10 cm water level than at the other water levels. In contrast, in *C. brevicuspis*; the two parameters did not differ significantly among the five water levels for this species – plant height ranged from 31.8 cm to 46.5 cm and tiller number ranged from 2.1 to 2.8 (Fig. 3).

Leaf length was lowest at 20 cm (22.3 cm) and highest at –10 cm (32.2 cm) in *I. cylindrica* and it was lowest at 20 cm (20.6 cm) and highest at 0 cm (27.1 cm) in *C. brevicuspis*. Leaf width was higher at –20 cm, –10 cm and 0 cm than at 10 cm and 20 cm in *I. cylindrica* and it was low at 20 cm, moderate at 10 cm and 0 cm, and high at –20 cm and –10 cm in *C. brevicuspis*.

For *I. cylindrica*, the ascending order for leaf area was 20 cm < 10 cm ≤ –20 cm ≤ 0 cm ≤ –10 cm (Fig. 3). For *C. brevicuspis*, leaf area was lowest at 20 cm, intermediate at 10 cm and 0 cm, and highest at –20 cm and –10 cm. For *I. cylindrica*, the ascending order for leaf number was 20 cm ≤ 10 cm ≤ 0 cm ≤ –20 cm ≤ –10 cm. For *C. brevicuspis*,

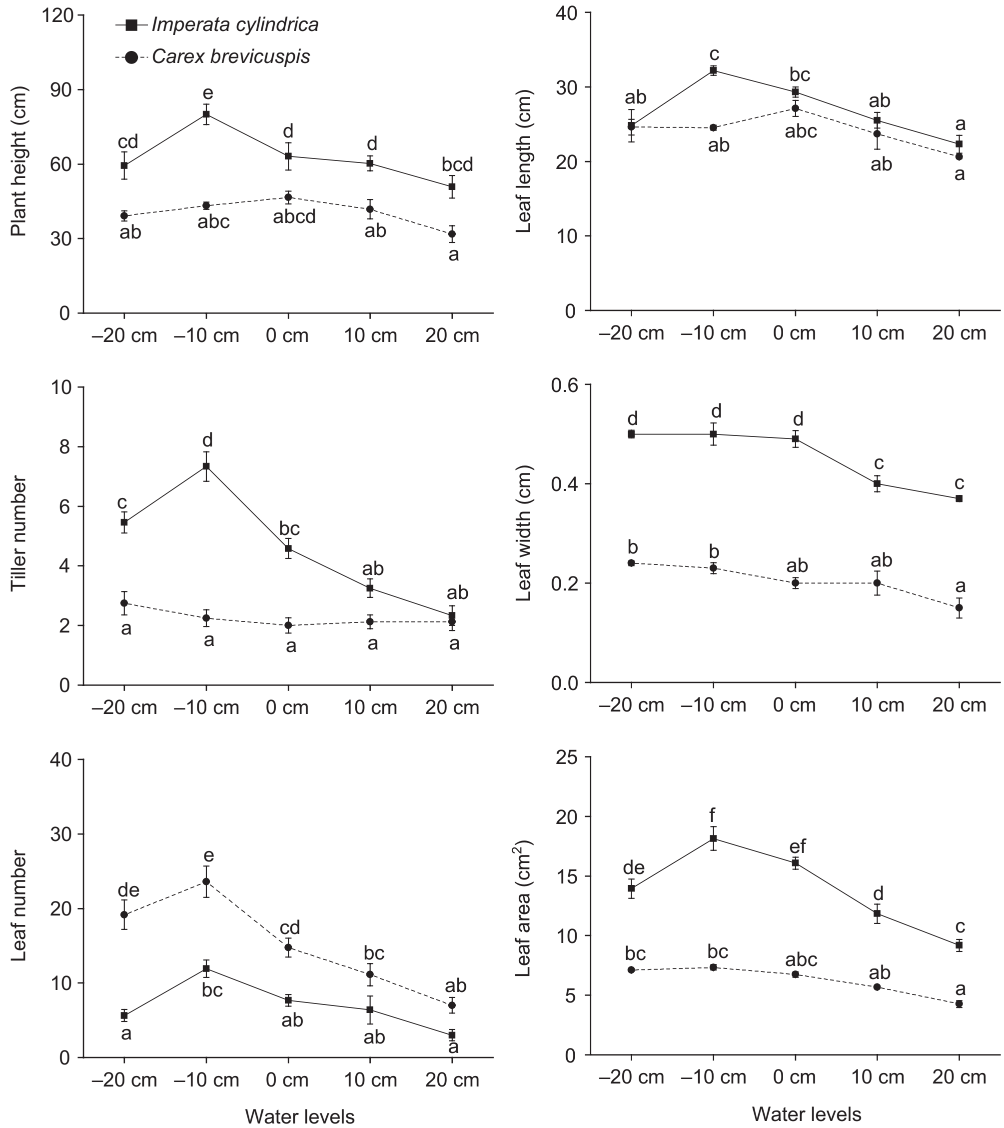

Figure 3. Aboveground morphological parameters (means ± SE) of two plant species (*Imperata cylindrica* and *Carex brevicuspis*) grown at five different water levels. Means not sharing a common letter differ significantly among treatments at $p < 0.05$ based on Tukey's test.

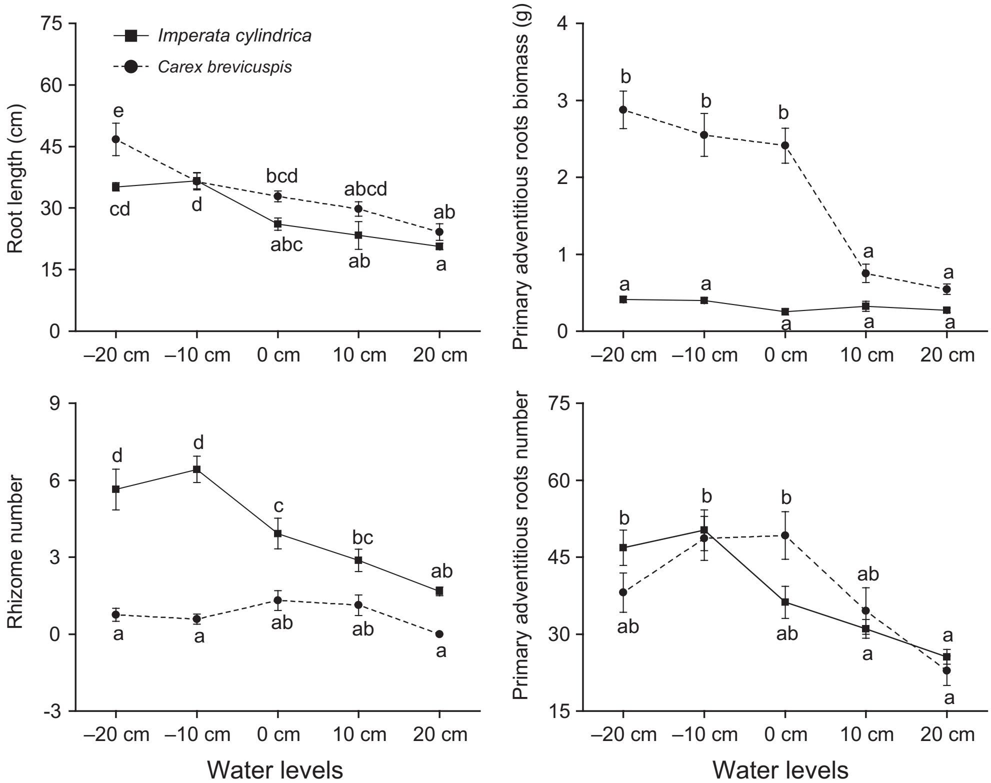

Figure 4. Root morphological parameters (means ± SE) of two plant species (*Imperata cylindrica* and *Carex brevicuspis*) grown at five different water levels. Means not sharing a common letter differ significantly among treatments at $p < 0.05$ based on Tukey's test.

there was little variation among treatments with the lowest values at 20 cm and –20 cm and the highest at –10 cm.

Belowground morphology

For *I. cylindrica*, root length and rhizome number were lowest at 20 cm, intermediate at 10 cm and 0 cm, and highest at –10 cm and –20 cm (Fig. 4). Root length increased with decreasing water level in *C. brevicuspis* but the rhizome number did not differ significantly among the five water levels.

For *I. cylindrica*, primary adventitious root biomass varied from 0.27 g to 0.41 g per plant and was not significantly different among the five water levels (Fig. 4). For *C. brevicuspis*, it ranged from 0.50 g to 2.88 g per plant and was significantly lower at 20 cm and 10 cm than at the other water levels. For *I. cylindrica*, the number of primary adventitious roots was higher at –20 cm and –10 cm than at 10 cm and 20 cm. For *C. brevicuspis*, the number of primary adventitious roots was higher at –10 cm and 0 cm than at 20 cm.

Discussion

Plant growth is significantly associated with water tolerance (van Eck et al. 2004, Li et al. 2013, Chen et al. 2015). In the present study, plant biomass was higher at the –10 cm water level than at the other levels (–20 cm, 0 cm, 10 cm and 20 cm) in both *Imperata cylindrica* and *Carex brevicuspis*. Thus, a –10 cm water level appear to be optimal for both species. However, when the water level rose from –10 cm to 0 cm, the decrease in plant biomass was greater in *I. cylindrica* than in *C. brevicuspis*. This results suggest that *I. cylindrica* has a lower flooding tolerance than *C. brevicuspis*. Based on the variation in plant biomass at different water levels, *C. brevicuspis* also had higher flooding tolerance than *Miscanthus sacchariflorus*, another emergent plant species in the Dongting Lake wetlands (Li et al. 2013). Low flooding tolerance in *I. cylindrica* may explain why it is mostly distributed at slightly higher elevations along the lake. In contrast, the higher flooding tolerance in *C. brevicuspis* could explain the preference of this species for lower elevations that flood.

Plant morphology may also be significantly correlated with water availability (Li et al. 2011a, Kirwan and Guntenspergen 2015). Under flooding conditions, plants tend to increase biomass allocation to aboveground tissues to increase access to light and oxygen (Jackson 2008, Kim et al. 2013). However, in the present study, plant height did not significantly differ among the –20 cm, 0 cm, 10 cm and 20 cm water levels. Similarily, Gimeno et al. (2012) found that flooding did not decrease *Jatropha curcas* seedling height. Along the water level gradient, *I. cylindrica* showed more variation in tiller number, leaf number, leaf length, leaf width and leaf area than did *C. brevicuspis,* indicating that *I. cylindrica* had a higher water sensitivity than *C. brevicuspis.* Under drought conditions, plants tend to increase biomass allocation to underground tissues in order to increase water uptake (Iwanaga and Yamamoto 2008, Li et al. 2011b). The present study showed that root length, rhizome number, and primary adventitious root biomass and number all increased with decreasing water level for *I. cylindrica*, however, neither rhizome number nor primary adventitious root biomass differed significantly among the five water levels for *C. brevicuspis*. This results also suggest that *I. cylindrica* has a higher water sensitivity than *C. brevicuspis.* Highly water-sensitive species are often distributed at higher elevations, whereas plants with lower water sensitivity tend to be found in lower elevation areas (Luo et al. 2008, Chen et al. 2015). Kano et al. (2011) showed that total root length in rice increased under mild drought conditions.

We may thus conclude from the present study that the low flooding tolerance and high water sensitivity of *I. cylindrica* may explain its distribution in higher elevation dry areas, while high flooding tolerance and low water sensitivity in *C. brevicuspis* may explain its distribution in lower elevation wet zones. In a previous study (Li et al. 2014), under soil drought conditions in poplar plantations in the Dongting Lake wetlands, *C. brevicuspis* decreased in abundance, while *I. cylindrica* increased.

Soil physicochemistry is also an important determinant of wetland plant distribution (Chen et al. 2015). Our results may, therefore, not fully account for the plant distribution patterns observed in the wetland. Future studies should integrate the combined influences of several parameters on wetland plant growth and should be conducted to elucidate all the mechanisms regulating plant zonation patterns in wetlands.

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