Competition between two wetland macrophytes under different levels of sediment saturation

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ABSTRACT

Plant-plant interactions have been widely studied under various environmental conditions. However, in wetland ecosystems how plant interactions change in response to variation in sediment saturation remains largely unclear, even though different levels of sediment saturation play important roles in determining plant growth performance in wetland ecosystems. To this end, a competition experiment with two typical wetland species, Carex brevicuspis *(neighbor plant) and* Polygonum hydropiper *(target plant), was conducted in a target-neighbor design. Two water levels (0 cm and -40 cm water levels representing waterlogged and drained sediments, respectively) and three neighbor plant densities (0 plants m⁻², 400 plants m⁻², and 1600 plants m⁻²) were tested in a factorial design. Biomass accumulation of* P. hydropiper *decreased along with enhanced* C. brevicuspis *density in the waterlogged treatment. However, in the drained treatment, biomass accumulation did not change under two* C. brevicuspis *densities. Above-ground relative neighbor effect index (ARNE) and relative neighbor effect index (RNE) of* C. brevicuspis *on* P. hydropiper *increased along with enhanced* C. brevicuspis *density only under waterlogged conditions. The below-ground relative neighbor effect index (BRNE) was not affected at the different water level and density treatments. The below-ground mass fraction of* P. hydropiper *was much higher in the waterlogged treatment than it was in the drained one, especially with no* C. brevicuspis *treatment. However, the leaf mass fraction displayed the opposite pattern. The longest root length of* P. hydropiper *was much shorter under waterlogged treatment than under the drained treatment. These results suggest that the competition intensity of* C. brevicuspis *to* P. hydropiper *increased along with increasing* C. brevicuspis *density only under waterlogged conditions. Moreover, this study also confirms that* P. hydropiper *can acclimate to water stress mainly through modulating its root architecture, for example reducing the root system length or increasing the root mass fraction.*

Key words: Sediment saturation gradient, stress-gradient hypothesis, interspecific competition, Carex brevicuspis, Polygonum hydropiper.

INTRODUCTION

Plant-plant interactions, including negative (competition or interference), neutral, and positive (facilitation) relationships, have been a focal issue in plant community ecology for decades (Michalet *et al*., 2006; Brooker *et al*., 2008). Competition involves a struggle to preempt resources, such as light, water, and nutrients, which consequently limit plant growth and restrict species distribution ranges by reducing their available niche (Grime, 2001). Conversely, facilitation promotes plants growth and potentially extends the geographical range of species (Michalet *et al*., 2006).

Studies have confirmed that the direction and intensity of interactions varied significantly according to gradients of abiotic factors, neighbor characteristics, and target plant traits (Pennings, *et al*., 2003; Luo *et al*., 2010). Furthermore, these changes play important roles in maintaining vegetation structure and dynamics (Gebauer *et al*.,

2002; Armas and Pugnaire, 2005). The relationship between plant interactions and the environment has been summarized as the stress-gradient hypothesis (SGH), which suggests that a shift from net negative towards net positive interactions can take place moving from benign to harsh environments (Callaway *et al*., 2002). To date, this hypothesis is supported by various studies conducted in a wide variety of ecosystems and different environmental gradients (Callaway *et al*., 2002; Luo *et al*., 2010). However, other studies have failed to confirm this hypothesis (Pennings *et al*., 2003; Gross *et al*., 2010). Therefore, the generality of this hypothesis need to be further tested (Maestre *et al*., 2005; Lortie and Callaway, 2006).

Wetland vegetation, especially that growing in river-connected lakes or floodplains, often experiences both drained and waterlogged sediment conditions (Grace, 1999; Pagter *et al*., 2005). Waterlogging could inhibit plant growth mainly due to the reduced oxygen availability and redox potential (Eh) in the sediment (Deegan *et*

al., 2007; Li *et al*., 2011). Generally, plants can acclimatize to waterlogged conditions through various morphological adaptations, such as increased allocation to roots, decreased root length, and formation of aerenchyma (Loreti and Oesterheld, 1996; Lenssen *et al*., 2003; Xie *et al*., 2008). These adaptations allow plants to acclimatize to anaerobic conditions by increasing oxygen transport to roots or by reducing radial oxygen loss to the sediment (Luo and Xie, 2009). Moreover, these adaptations depend on the duration of waterlogging, variability in environmental factors (*e.g*., pore water oxygen and nutrient availability, redox potential) and, plant development (Ribaudo *et al*., 2011; Soana and Bartoli, 2014). Plant interactions under various abiotic factors have been widely studied, and include water availability (Luo *et al*., 2010; Weigelt *et al*., 2000; Zhang *et al*., 2014), sedimentation (Franks and Peterson, 2003), and salinity (Mesléard *et al*., 1993). However, the mechanisms of plant-plant interactions differ significantly under vary environmental stresses and require further studies.

The aim of this experiment was to elucidate how the intensity of interspecific competition changes in response to drained and waterlogged sediment conditions. To this end, at Dongting Lake, a competition experiment between the two local dominant wetland species (*Carex brevicuspis* C. B. Clarke and *Polygonum hydropiper* Linn) was conducted using a target-neighbor design. *P. hydropiper*, as the target plant, was grown at two water levels and three *C. brevicuspis* densities (under six different experimental treatments). Biomass accumulation, above-ground relative neighbor effect index (ARNE), below-ground relative neighbor effect index (BRNE), relative neighbor effect index (RNE) of *C. brevicuspis* on *P. hydropiper* , biomass allocation and the longest root length of *P. hydropiper* were investigated to test the following hypotheses: i) the growth performance of *P. hydropiper* was significantly inhibited by waterlogged treatments. Moreover, the longest root length would be reduced but root mass fraction would be increased in the waterlogged treatment; ii) higher neighbor density would inhibit the growth performance of *P. hydropiper*; iii) growth performance and competition intensity would be altered when *P. hydropiper* was subjected to competition and waterlogged conditions simultaneously.

METHODS

Study area

Dongting Lake (28°30'-30°20' N, 111°40'-113°10' E), the second largest freshwater lake in China with an area of 2620 km^2, is located in the northern Hunan Province in a basin south of the Yangtze River, to which it is connected by three distributary channels (Pan *et al*., 2014; Fig. 1). The mean annual temperature in this wetland is 16.4-17°C, with the lowest (*i.e*., 3.9-4.5°C) and highest (*i.e*., 28.6-29.1°C) temperatures in January and July, respectively. Annual pre-

Fig. 1. Location map of Dongting Lake, China.

cipitation is 1382 mm, with more than 60% falling between April and August. This lake is characterized by large seasonal fluctuations in water level; it is completely flooded during May-October and drained during November-April. In this lake, wetland plants usually distribute along the water-level gradient (high-elevation species *Miscanthus sacchariflorus* (Maxim.) Benth, middle-elevation species *C. brevicuspis* and *P. hydropiper*, and low-elevation species *Phalaris arundinacea* Linn). Typically, *C. brevicuspis* forms large patches of mono-dominant communities or is co-dominated with other *Carex* species or *P. hydropiper*, while *P. hydropiper* is usually co-dominate with *Carex* species (Peng *et al*., 1984).

In recent years, particularly after construction of the Three Gorge Dam, the structure of plant communities has changed significantly in the Dongting Lake (Li *et al*., 2013). We (staff of Dongting Lake Station for Wetland Ecosystem Research, Chinese Academy of Sciences) found that large areas of *P. hydropiper* have disappeared during our annual field investigations. However, the mechanism of *P. hydropiper* loss is far from clear.

Plant materials

C. brevicuspis, a perennial rhizomatous sedge, is a widespread wetland species found in eastern mainland China and Taiwan (Dai *et al*., 2010). The pseudoculm of the plant, made up of a series of overlapping leaf sheaths, is usually 20-55 cm in height. *P. hydropiper* (Polygonaceae) was described as a cosmopolitan annual herb (Li *et al*., 2013). The leaves of *P. hydropiper* tend to be wavy at the edges, and the plant often has a reddish appearance. Fibrous roots usually grow on the internodes of belowground rhizomes (Hobbs, 1992). At the Dongting Lake, the two species flower and fruit from April to May before flooding occurs, and both recruit mainly through producing vegetative ramets emerging from underground rhizomes (Chen *et al*., 2011; Li *et al*., 2014).

Plants（*C. brevicuspis* and *P. hydropiper*）were collected in February, 2011 from Junshan County (112°59'40.0'' E; 29°22'17.7'' N; East Dongting Lake) extracting small blocks of colonized sediments (20 cm×20 cm), which were subsequently transported to an experimental field in the Institute of Subtropical Agriculture (at the Chinese Academy of Sciences). Plant fragments with roots were placed into plastic buckets, filled with a 15-cm sediment layer (collected from a mixed community of *P. hydropiper* and *C. brevicuspis*, containing 1.45% organic matter, 4.04 µg g^{-1} exchangeable N, and 0.88 µg g^{-1} exchangeable P) to favor the development of new ramets. The plastic buckets were placed in an outdoor area under natural light and the plants were watered with tap water (containing 0.511 µg L^{-1} NH$_4^+$-N, 1.760 µg L^{-1} NO$_3^-$-N and 0.527 µg L^{-1} PO$_4^{3+}$-P, pH=7.2) when necessary.

Experimental set-up

The experiment combined two water levels (0 and -40 cm) with three *C. brevicuspis* densities (no neighboring plants, 0 plants m^{-2}, medium neighbor density, 400 plants m^{-2}, and high neighbor density, 1600 plants m^{-2}) in a factorial design with four replicates, according to our field investigation (density ranged from 300-2000 plants m^{-2}). Therefore, the experiment included six treatments: two single-individual treatments (one plant of *P. hydropiper* per water level) and four mixed-species treatments (one plant of *P. hydropiper* as the target plants, and 25 plants or 100 plants of *C. brevicuspis* arranged in a 25 cm×25 cm square array as the neighboring plants per water level). A total of 1024 ramets (24 for *P. hydropiper* and 1000 for *C. brevicuspis*) of similar size (3-4 leaves, about 25 cm in height for *C. brevicuspis* and 6-7 leaves, about 23 cm in height for *P. hydropiper*) were cut from plant cultures on 8th June, 2011. They were planted in PVC tubes (45 cm in height and 30 cm in diameter) filled with 45 cm of the same soil used for plant incubation.

Six tubes (one tube per treatment) were placed into each of four larger plastic bins (98 cm×76 cm×68 cm) to control water level. The plastic bins were placed in an outdoor area under natural light in the Institute of Subtropical Agriculture, the Chinese Academy of Sciences (Changsha, Hunan province). Different water levels were obtained by elevating the PVC tubes with cement bricks. Experimental treatments began 7 days after planting and two water levels were used: -40 cm (drained treatment design based on our field investigation, relative to the soil surface) and 0 cm (waterlogged treatment, relative to the soil surface). The water table of *P. hydropiper* was 59±9 cm during our 2 years field investigation (unpublished data). Tap water was timely supplied and surplus water was removed after rains to control water level. We also replenished the water once a week to prevent algae growth.

The plants were harvested following 3-months of treatment. Plant roots were carefully dug out by hand and cleaned with tap water. First, the longest root length, an important index that reflects the plants ability to acclimatize to changes in water availability, was measured using a 0.1 cm ruler (Xie *et al*., 2008). Next, plants were divided into leaves, shoots, and below-ground parts (rhizomes and roots), oven dried at 80°C for 48 h, and weighed. Biomass accumulation was calculated as the collective mass of all tissues. Leaf mass fraction, stem mass fraction, and below-ground mass fraction were determined as the ratios of leaf mass, stem mass and below-ground mass to biomass accumulation, respectively.

Relative neighbor effect index

Intensity of interspecific competition was quantified

using the relative neighbor effect index (RNE; Markham and Chanway, 1996):

$$RNE = (P_{-N} - P_{+N})/X \qquad \text{(eq. 1)}$$

where P is the final biomass in the presence (+N) and absence (−N) of neighbors, and X the larger value of P_{-N} or P_{+N}. Moreover, we also calculated the below-ground relative neighbor effect (BRNE) and the above-ground relative neighbor effect (ARNE) based on the final below-ground mass and above-ground mass, respectively. Calculations were performed using Ln(x+1)-transformed biomass data (Belcher *et al.*, 1995). RNE is an improved version of the relative competitive intensity index (Wilson and Keddy, 1986; Belcher *et al.*, 1995). The RNE enables both competitive and facilitative interactions to be quantified without bias on a scale of -1 to +1. A value of 0 indicates no interaction, a negative value indicates facilitation, and a positive value indicates competition. However, the RNE measures the outcome of competition without regard to habitat or environmental conditions (Wilson, 2007).

Data analysis

Two-way ANOVAs, with water level and neighbor plant density as the main factors, were performed to determine the main effects and interactions on the biomass accumulation, RNE, BRNE and ARNE of *C. brevicuspis* on *P. hydropiper*, biomass allocation, and the longest root length of *P. hydropiper*. Multiple comparisons of means were performed by Tukey's test at the 0.05 significance level and a Bonferroni correction for multiple comparisons was made where necessary. Data were $\log_{10}$-transformed if necessary to reduce heterogeneity of variance. Normality and homogeneity were tested using Liljefors test and Levene's test, respectively. All analyses were performed using the software SPSS 16.0 for Windows (SPSS Inc., USA).

RESULTS

Both water level (P<0.05; F=27.896; Fig. 2) and *C. brevicuspis* density (P<0.05; F=46.128; Fig. 2) had a significant effect on the biomass accumulation of *P. hydropiper*, which was highest in the -40 cm water level + no neighboring plants treatment (40.5±1.73 g per plant) and lowest in the 0 cm water level + high neighbor density treatment (7.6±1.79 g per plant). Moreover, biomass accumulation of *P. hydropiper* decreased significantly with increments of *C. brevicuspis* density in the waterlogged treatments. However, in the drained treatments, biomass accumulation of *P. hydropiper* had similar patterns at the medium and high *C. brevicuspis* densities.

The ARNE (P<0.05; F=5.262; Fig. 3) and RNE

(P<0.05; F=13.734; Fig. 3) of *C. brevicuspis* on *P. hydropiper* were significantly affected by *C. brevicuspis* density. However, both *C. brevicuspis* density (P>0.05; F=0.001; Fig. 3) and water level (P>0.05; F=2.440; Fig. 3) had an insignificant influence on the BRNE of *C. brevicuspis* on *P. hydropiper*. In the waterlogged treatment, the ARNE and RNE of *C. brevicuspis* on *P. hydropiper* increased significantly along with enhanced density. However, the effect of *C. brevicuspis* density on the ARNE (P>0.05; F=0.050; Fig. 3) and RNE (P>0.05; F=0.406; Fig. 3) of *C. brevicuspis* on *P. hydropiper* was insignificant in the drained treatment. The below-ground mass fraction of *P. hydropiper* was significantly influenced by water level (P<0.05; F=7.675; Tab. 1) and *C. brevicuspis* density (P<0.05; F=5.895; Tab. 1). At the same *C. brevicuspis* density, the below-ground mass fraction of *P. hydropiper* was significantly higher in the waterlogged treatment than in the drained one, especially with no *C. brevicuspis* treatment. The leaf mass fraction of *P. hydropiper* was only affected by water level (P<0.05; F=30.238; Tab. 1), which was much higher in the drained treatment than in the waterlogged one. The stem mass fraction of *P. hydropiper* was insignificantly influenced by both water level (P>0.05; F=2.724; Tab. 1) and *C. brevicuspis* density (P>0.05; F=2.525; Tab. 1).

The longest root length of *P. hydropiper* was much shorter in the waterlogged treatment (15.3-20.0 cm) than in the drained one (37.3-42.0 cm; P<0.05; F=37.364; Fig. 4). However, the effect of density was insignificant (P>0.05; F=0.848; Fig. 4).
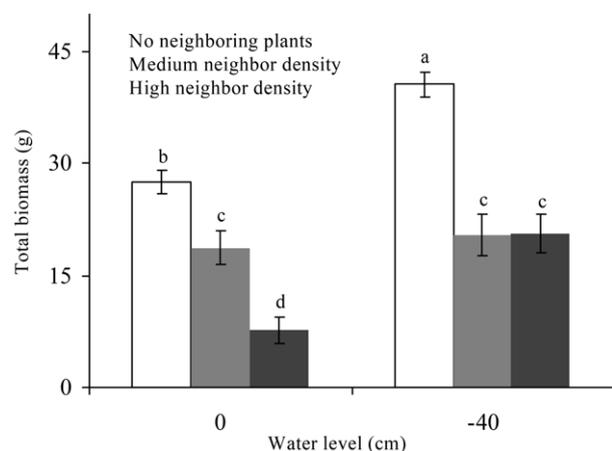

Fig. 2. Biomass accumulation (means±SE, n=4) of *Polygonum hydropiper* growing under three *Carex brevicuspis* densities (no neighboring plants, 400 plants m⁻², 1600 plants m⁻²) and two water levels (0 cm and -40 cm, waterlogged and drained conditions). Different letters indicate significant differences between treatments at the 0.05 significance level.

DISCUSSION

When individual *P. hydropiper* were planted, a lower biomass accumulation was recorded in the drained treatments than in the waterlogged treatment. This observation
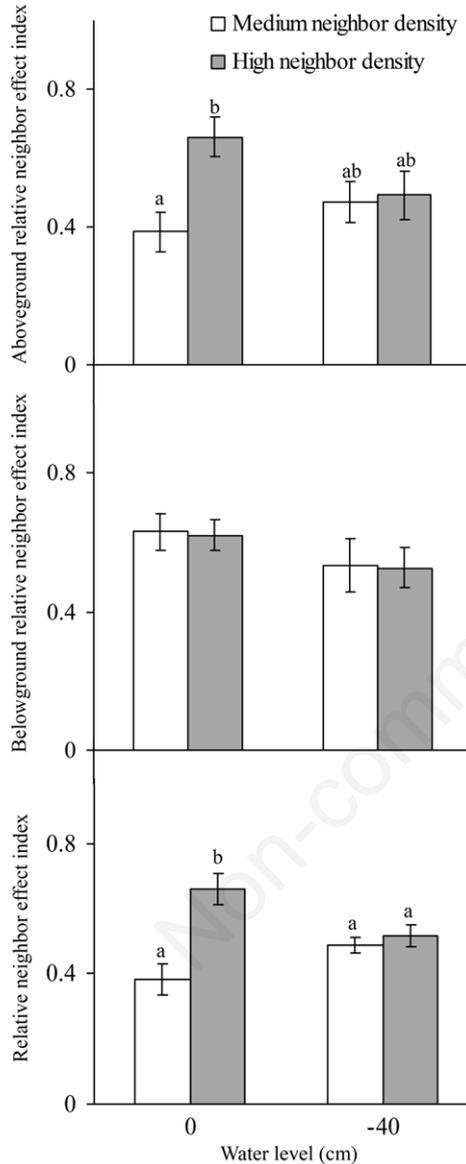

Fig. 3. Aboveground relative neighbor effect index (ARNE, means±SE, n=4), belowground relative neighbor effect index (BRNE, means±SE, n=4), and relative neighbor effect index (RNE, means±SE, n=4) of *Polygonum hydropiper* growing under different *Carex brevicuspis* densities (no neighboring plants, 400 plants m^{-2}, 1600 plants m^{-2}) and two water levels (0 cm and -40 cm, waterlogged and drained conditions). Different letters indicate significant differences between treatments at the 0.05 significance level. ARNE, BRNE, and RNE were calculated based on the final aboveground biomass, belowground biomass, and total biomass in the presence and absence of neighbors, respectively.

suggests that the growth of *P. hydropiper* was significantly inhibited by waterlogging. This is consistent with our first hypothesis: *P. hydropiper* is an annual species that can grow in terrestrial or shallow flooded habitats such as riverbanks, stream sides, and wet valleys. Furthermore, it might growth better in elevated areas than in shallow-flooded habitats (Li *et al*., 2013). Actually, sediment waterlogging has long been identified as a major abiotic stress and the constraints it imposes on roots have marked effects on plant growth and development (Parent *et al*., 2008).

Our data support the idea that during long-term evolutionary acclimatization, *P. hydropiper* might have been acclimatized to waterlogging stress through its morphological and physiological adaptations, such as decreased root length and altered biomass allocation patterns. Indeed, our study verified that the longest root length of *P. hydropiper* recorded at the waterlogged treatment was significantly lower than that measured in the drained treatments. This is probably a response to sediment anoxia/hypoxia in agreement with those observed by Xie *et al*. (2008). Shorter root length is beneficial for plant survival and maintains root activity under water-saturated environments, since the top layer of sediment usually has higher oxygen contents and Eh values (Wheeler, 1999; Xie *et al*., 2008). Moreover, our results also confirm that the below-ground mass fraction was much higher in the waterlogged treatments than in drained treatments. In waterlogged sediments, roots of both tolerant and intolerant species may serve as a carbohydrate sink and thus inhibit the investment in the above-ground plant organs (Lenssen *et al*., 2003), which might be beneficial to plants in preventing oxygenation of the entire root system, as has been
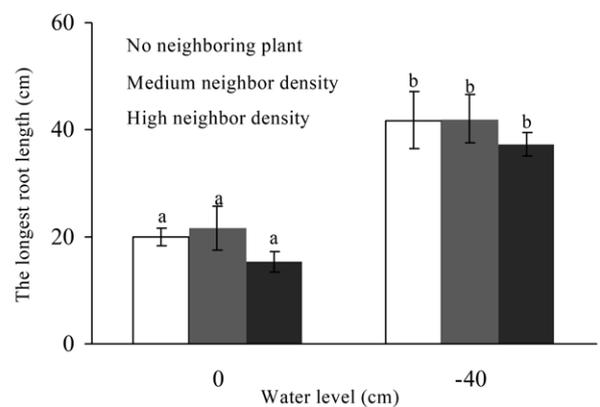

Fig. 4. The longest root length (means±SE, n=4) of *Polygonum hydropiper* growing under three *Carex brevicuspis* densities (no neighboring plants, 400 plants m^{-2}, 1600 plants m^{-2}) and two water levels (0 cm and -40 cm, waterlogged and drained conditions). Different letters indicate significant differences between treatments at the 0.05 significance level.

Tab. 1. Biomass allocation (means±SE, n=4) of *Polygonum hydropiper* growing under three *Carex brevicuspis* densities (no neighboring plants, 400 plants m⁻², and 1600 plants m⁻²) and two water levels (0 cm and -40 cm, waterlogged and drained conditions).

Water level (cm)	*C. brevicuspis* densities (plants m⁻²)	Leaf mass fraction	Stem mass fraction	Below – ground mass fraction
0	0	32.16±3.98[b]	33.22±2.77[ab]	34.62±1.27[a]
0	400	31.68±1.23[b]	42.08±4.85[a]	26.24±3.82[bc]
0	1600	28.10±1.58[b]	39.57±2.37[ab]	32.33±1.25[ab]
-40	0	39.81±0.38[a]	33.97±0.97[ab]	26.22±0.62[bc]
-40	400	41.16±1.64[a]	36.76±1.02[ab]	22.08±2.52[c]
-40	1600	38.44±1.05[a]	32.79±0.90[b]	28.77±1.78[abc]

[a–c]*Different letters indicate significant difference among treatments at the 0.05 significance level.*

previously reported by Visser *et al*. (2000). However, our results contradict, in part, to the results of Kalapos *et al*. (1996), which found that plant root could be stimulated to grow under soil drying conditions. The difference might be accounted for by different water availabilities. In our experiment, water was not a limiting factor influencing the growth of *P. hydropiper* due to its higher root length in the drained treatment. Therefore, a higher root mass fraction was not observed in the drained treatment.

The relationship between interspecific competition and plant growth has been widely examined and showed that increased densities could reduce plant growth due to lower resource availability (Grace and Tilman, 1990; Davis *et al*., 2009). In this study, biomass accumulation of *P. hydropiper* decreased significantly along with increasing *C. brevicuspis* densities in waterlogged treatments. Moreover, the ARNE and RNE of *C. brevicuspis* on *P. hydropiper* also increased significantly with increasing *C. brevicuspis* densities in the waterlogged treatments. These results are consistent with our second hypothesis, and suggest that a higher *C. brevicuspis* density intensifies competition for light and available growth space in the waterlogged treatment. Consequently, a limited growth of *P. hydropiper* was observed, in agreement with those suggested from previous studies (Davis *et al*., 2009; Luo *et al*., 2010). However, similar BRNE patterns at different *C. brevicuspis* densities suggested that competition between *C. brevicuspis* to *P. hydropiper* is mainly associated with light competition rather than with nutrient availability.

Similar biomass accumulation, ARNE, BRNE, and RNE at different *C. brevicuspis* densities in the drained treatments suggest that the intensity of competition was reduced in the drained condition In fact, plant competition that is dependent on the intensity of environmental stress has been long studied by ecologists (Brooker *et al*., 2008; Luo *et al*., 2010). Luo *et al*. (2010) found that the intensity of intra- and interspecific competition decreased, while the intensity of facilitation increased, with increasing water levels among three typical marsh plants in the Sanjiang Plain. The higher sensitivity of *C. brevicuspis* to water availability compared to *P. hydropiper* might ex-

plain the growth performance of the latter in the drained treatment (Li *et al*., 2013). During 7 years of field investigation, we (the researchers in the Dongting Lake Station for Wetland Ecosystem Research, the Chinese Academy of Sciences) found that the maximum root depth of *C. brevicuspis* was less than 20 cm. Therefore, the growth of *C. brevicuspis* might be significantly limited at the -40 cm water level, consequently, resulting in lower levels of competition with *P. hydropiper*. At the end of the experiment, we also found that many *C. brevicuspis* leaves were withered, which led to reduced interspecific competition for light, supported by the above-ground relative neighbor effect as occurred in the drained treatment.

CONCLUSIONS

In conclusion, our study confirmed that the intensity of competition between *C. brevicuspis* to *P. hydropiper* increased along with increasing *C. brevicuspis* density in the waterlogged treatment, while there was no significant change between the two *C. brevicuspis* densities in the drained treatment. Moreover, our study also suggested that *P. hydropiper* could acclimate to waterlogged stress by modulating its root architecture, such as reducing the root system length or increasing the root mass fraction. In recent years, the *P. hydropiper* community has been seriously degraded in association with the changing hydrological regimes in the Dongting Lake, leading to a significant reduction of biodiversity in the lake. In this context, present data provide experimental information on the role of competition in structuring the dynamics of wetland plant communities and may assist with the effective management of regulated lakes or reservoirs such as the Dongting Lake.

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