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Short communication

Increased density facilitates plant acclimation to drought stress in the emergent macrophyte *Polygonum hydropiper*

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ABSTRACT

Wetland plants frequently experience drought events due to large water level fluctuations; drought might present a greater limitation to plant survival than flooding in many wetlands. High plant density can increase the relative humidity, which might facilitate the acclimation of plants to drought stress. However, studies on the effects of plant density on acclimation to drought are scarce. This study aimed to elucidate the influence of density on plant response to drought stress by investigating morphological and physiological characteristics of *Polygonum hydropiper* L. var. *flaccidum*, one of the dominant species in the Dongting Lake wetland, China. Experimental greenhouse treatments, including three density (16, 144, and 400 plants m^{-2}) and three water level (0, −20, and −40 cm relative to the soil surface) treatments, were performed in a factorial design. Soil water content increased with increasing water level and plant density. In the 0- and −20 cm water level treatments, biomass accumulation per plant decreased significantly with increasing density. However, in the −40 cm treatment, biomass accumulation did not change among the three plant densities. Higher density and water level led to lower leaf mass fraction. Both electrolyte leakage and malondialdehyde (MDA) content increased along with decrease in water level. Moreover, they showed no change with plant density in the 0- and −20 cm water level treatments, but decreased with increased density in the −40 cm treatment. Soluble sugar content increased with decreasing water level and increasing density, whereas starch content decreased significantly with decreasing water level. These data indicate that a higher density facilitates the acclimation of *P. hydropiper* to drought stress. Moreover, our results might reveal the important role of density in the restoration of *P. hydropiper* communities.

1. Introduction

Many natural wetlands are maintained primarily by large seasonal fluctuations in water level, such as complete inundation during wet parts of the year interspersed with prolonged dry periods (Parolin et al., 2010; Li et al., 2013). The tolerance or sensitivity of wetland plants to these hydrologic extremes is important to determine their survival and distribution (Pagter et al., 2005). The influence of flooding on the growth, distribution, and composition of wetland macrophytes has been studied in detail (Luo et al., 2010; Li et al., 2011). However, the role of dry periods has been investigated less thoroughly, although this factor might have a greater impact on plant survival than flooding in many wetlands (Lopez and Kursar, 2007).

Drought adversely influences the growth and metabolism of wetland plants by stimulating increased production of superoxides such as malondialdehyde (MDA) or hydrogen peroxide (Luo et al., 2008; Zhao et al., 2008), and by leading to a decline in photosynthetic activity (Pagter et al., 2005). Generally, plants can tolerate or avoid drought stress through morphological, physiological, and phenological mechanisms such as adjustment of biomass allocation; modification of root length; adjustment of osmotic potential; and enhancement of MDA, proline, soluble sugar, and antioxidative enzyme contents (Bartels and Sunkar, 2005; Xie et al., 2008; Li et al.,

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2013). These adjustments are beneficial for plants to improve their water-absorbing capacity and to resist desiccation or alleviate lipid peroxidation (Bartels and Sunkar, 2005). Moreover, these adjustments depend on the drought severity and duration, plant genotype and developmental stage, and environmental factors (Pagter et al., 2005).

The role of density in maintaining vegetation structure and population dynamics has been extensively investigated (Jiang et al., 2008; Li et al., 2009; Ala et al., 2014). Generally, plant growth can be inhibited in densely occupied habitats due to the competition for resources such as light and nutrients (Shilo-Volin et al., 2005). *Lemna minor* and *Spartina anglica* were shown to exhibit growth limitation or death at densities above 400–700 plants m^{-2} and 81 plants m^{-2}, respectively (Driever et al., 2005; Li et al., 2009). However, a dense canopy also has positive effects on plant growth, particularly under severe environmental conditions (Franks and Peterson, 2003; Luo et al., 2010). When treated with 40 cm water level, performances of three marsh plants were considerably better in high density treatments, since high plant density produced a relatively oxygen-rich environment (Luo et al., 2010). Physical and physiological effects of wind were ameliorated by higher density in *Sinapis alba* (Retuerto et al., 1996). High density might also facilitate plant acclimation to drought stress, since relative humidity and leaf wetness duration could be increased by reduced air movement and light penetration (Tu, 1997; Asghari et al., 2009). However, this positive effect requires further study.

Dongting Lake (28°30′–30°20′N, 111°40′–113°10′E) is the second-largest and the most typical river-connected lake in China. The wetlands in this lake are characterized by large seasonal fluctuations in water level; they are completely flooded during May to October and remain dry during November to April. In recent years, drought episodes have occurred frequently in the Dongting Lake ecosystem, leading to significant changes in the structure of plant communities (Li et al., 2013). In particular, during our annual field investigation, we (the staff of Dongting Lake Station for Wetland Ecosystem Research, the Chinese Academy of Sciences) found that *Polygonum hydropiper* community had degraded seriously in areas such as the lake shores of Chanpanzhou and Beizhouzi.

This study aimed to determine whether increased plant density could facilitate plant acclimation to drought stress. For this, a dominant wetland plant of Dongting Lake, *P. hydropiper*, was grown at three densities under three water levels, and morphological (biomass accumulation and allocation) and physiological (electrolyte leakage and contents of MDA, soluble sugar, and starch) characteristics were investigated to test the following hypotheses: (1) both drought and high-density treatment will lead to lower biomass accumulation of *P. hydropiper*, and the influence of drought will be stronger in the low-density than in the high-density treatments; (2) drought will lead to a higher belowground mass fraction but lower leaf and stem mass fraction for *P. hydropiper*, and these changes will be stronger in the low-density than in the high-density treatments; (3) electrolyte leakage and MDA and soluble sugar contents of *P. hydropiper* will increase, but starch content will decrease in the drought treatment, and there will be less evidence of these changes in the high-density than in the low-density treatments.

2. Materials and methods

2.1. Plant materials

P. hydropiper can form large patches of monodominant communities or occur as a codominant species with *Carex* species in Dongting Lake (Peng et al., 1984). This species normally flowers and fruits from April to May before the period of flooding, and the recruitment of this species mainly occurs by producing vegetative ramets from rhizomes (Chen et al., 2011).

Ramets of *P. hydropiper* were collected in March 2012 from a monodominant stand in Chunfeng Village (29°13′49.72″N, 113°02′32.79″E), East Dongting Lake wetlands. The vegetation was cut into small blocks (20 × 20 cm) and transported to a greenhouse at the Institute of Subtropical Agriculture, the Chinese Academy of Sciences. New ramets were germinated by placing plant fragments with roots into plastic buckets containing 15 cm soil (1.87% organic matter, 28.5 $\mu g\,g^{-1}$ total N, and 7.83 $\mu g\,g^{-1}$ total P) collected from the *P. hydropiper* community. The temperature was controlled at 25 ± 2 °C during the day and 17 ± 2 °C at night. Light was provided using 400 W SON-T ARGO sodium lamps (Phillips, Guildford, UK) at a photon flux density of 600 $\mu mol\,m^{-2}\,s^{-1}$ (physiologically active radiation) for a 14-h photoperiod. Tap water (containing 0.511 $\mu g\,L^{-1}$ NH_4^+-N, 1.760 $\mu g\,L^{-1}$ NO_3^--N, and 0.527 $\mu g\,L^{-1}$ PO_4^{3+}-P, pH = 7.2) was supplied daily.

2.2. Experimental set-up

The experiment included three water levels (0, −20, and −40 cm relative to the soil surface) with three densities (low, 16 plants m^{-2}; medium, 144 plants m^{-2}; and high, 400 plants m^{-2}; field density ranged from 25 to 390 plants m^{-2}) in a factorial design with three replicates. In all, the experiment included nine treatments: three single-individual treatments (one plant per water level) and six multi-individual treatments (9 or 25 plants per water level, with the individual in the center designated as the target plant). A total of 630 similar-sized ramets (6–7 leaves, approximately 23 cm high) were cut from plant cultures on April 15, 2012. These ramets were planted in polyvinyl chloride tubes (45 cm high × 30 cm diameter) filled with 45 cm of the same soil used for plant incubation. Six tubes (two tubes per density treatment) were placed in each of nine larger plastic basins (98 × 76 × 68 cm) to control the water level.

After planting, the water level in all the basins was maintained at 45 cm depth for 1 week, after which it was adjusted to the required level. Water depth was adjusted weekly during the experimental period, and tap water was supplied as necessary. The entire volume of water was replaced every 2 weeks to prevent algal growth, and the water content of each tube was measured monthly by using a soil water analyzer (TZS-2X; Zhengjiang).2.2.1 Harvest and measurement of physiological indexes

The plants were harvested after 6 months. First, fresh leaf samples were collected for the analysis of physiological traits, and roots were carefully removed from the soil and cleaned using tap water. Plants were then divided into leaves, shoots, and belowground parts (rhizomes and roots), oven dried at 80 °C for 48 h, and weighed. Leaf mass removed for analysis of physiological traits was added to the corresponding plant biomass by converting fresh weight to dry weight. Leaf, stem and belowground mass fractions were determined as the ratios of leaf mass, stem mass, and belowground mass (rhizome and root) to total biomass, respectively.

Electrolyte leakage was determined as described by Dionisio-Sese and Tobita (1998). The content of MDA was measured using the method described by Duan et al. (2005). Dry leaf samples were used for soluble sugar and starch content analysis according to the methodology described by Yemm and Willis (1954).

2.3. Data analysis

For each basin, the mean values of two tubes per density treatment were used for the data analysis. Repeated-measures analysis of variance (ANOVA), with water level and density as dependent factors and time as a repeated-measures factor, was used to evaluate treatment effects on soil water content. Two-way ANOVA,

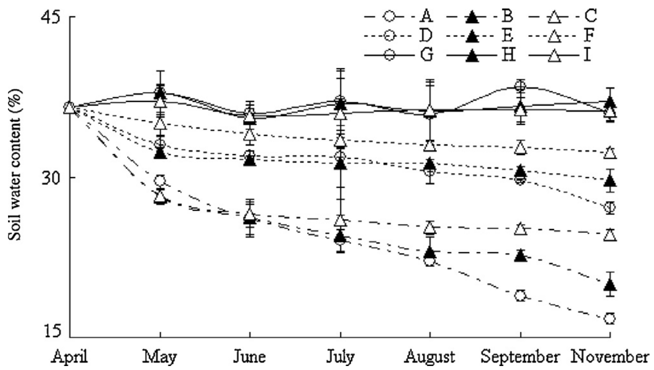

Fig. 1. Soil water contents of the nine treatments during the experimental period. Measurements were vertically dispersed through the 12-cm soil profile. Treatment A: −40 cm water level + low-density treatment; Treatment B: −40 cm water level + medium-density treatment; Treatment C: −40-cm water level + high-density treatment; Treatment D: −20 cm water level + low-density treatment; Treatment E: −20 cm water level + medium-density treatment; Treatment F: −20 cm water level + high-density treatment; Treatment G: 0 cm water level + low-density treatment; Treatment H: 0 cm water level + medium-density treatment; Treatment I: 0 cm water level + high-density treatment.

with water level and density as main factors, was used to determine the main effects and interactions on biomass accumulation, biomass allocation, electrolyte leakage, MDA content, soluble sugar content, and starch content. Multiple comparisons of means were performed using Tukey's test at the 0.05 significance level, and a Bonferroni correction was made where necessary. Data were $\log_{10}$-transformed if necessary to reduce heterogeneity of variances. Normality and homogeneity were tested using Liljefors and Levene's tests, respectively. All analyses were performed using SPSS software version 16.0 for Windows.

3. Results

3.1. Soil water content

Soil water content increased significantly with increased water level ($P < 0.05$; $F = 378.090$; Fig. 1) and density ($P < 0.05$; $F = 7.729$; Fig. 1). At the end of the experiment, soil water content did not differ significantly among the three density treatments at the 0 cm water level; on the other hand, at the −20 and −40 cm water levels, soil water content was 1.2 and 1.5 times higher in the high-density than in the low-density treatment, respectively.

3.2. Biomass accumulation

Water level ($P < 0.05$; $F = 4.424$; Fig. 2), density ($P < 0.05$; $F = 221.401$; Fig. 2), and their interactions ($P < 0.05$; $F = 4.110$) had significant effects on biomass accumulation, which was the highest (5.4 g/plant) in the −20 cm water level + low-density treatment and the lowest (1.3 g/plant) in the −20 cm water level + high-density treatment. In the −40 cm water level treatment, *P. hydropiper* showed similar growth performance among the different density treatments, whereas, for the other two water levels, growth performance decreased with an increase in density.

3.3. Biomass allocation

Higher density ($P < 0.05$; $F = 8.415$; Fig. 3) and water level ($P < 0.05$; $F = 16.041$; Fig. 3) led to lower leaf mass fraction. However, root and stem mass fractions showed insignificant changes across different treatments ($P > 0.05$; Fig. 3).

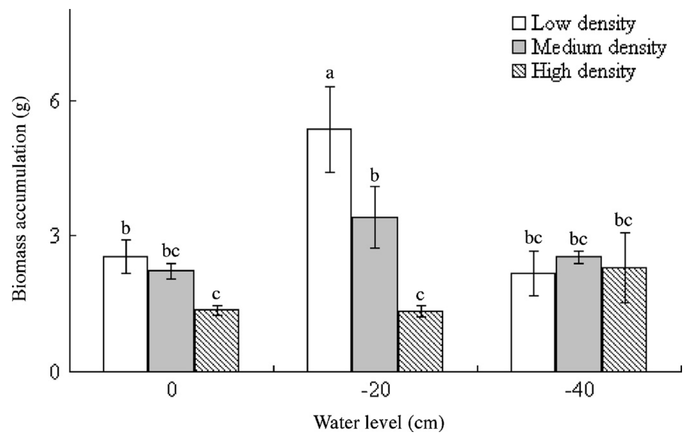

Fig. 2. Biomass accumulation (means ± standard error (SE), $n = 3$) of *Polygonum hydropiper* grown in three densities under three water levels. Different letters indicate significant differences among treatments at the 0.05 significance level.

3.4. Electrolyte leakage and MDA content

Electrolyte leakage was significantly influenced by water level ($P < 0.05$; $F = 80.410$; Fig. 4), plant density ($P < 0.05$; $F = 6.822$; Fig. 4), and their interactions ($P < 0.05$; $F = 11.042$); it was the highest in the −40 cm water level + low-density treatment (19.7%) and the lowest in the 0 cm water level + low-density treatment (9.50%). Moreover, electrolyte leakage showed insignificant changes with density in the 0-cm and −20-cm treatments, whereas it decreased along with increased plant density at the −40-cm water level.

MDA content increased significantly with decreased water level ($P < 0.05$; $F = 58.651$; Fig. 4). Moreover, in the −40 cm water-level treatment, MDA content decreased significantly with increasing plant density, whereas in the other two water level treatments, density had an insignificant influence on MDA content.

3.5. Contents of soluble sugar and starch

Soluble sugar content increased significantly with decreasing water level ($P < 0.05$; $F = 31.520$; Fig. 4) and increasing plant density ($P < 0.05$; $F = 4.817$; Fig. 4); sugar content was the highest (44.8 mg g^{-1}) in the −40 cm water level + high-density treatment and the lowest (28.8 mg g^{-1}) in the 0 cm water level + low-density treatment.

Starch content was lower in the low water level treatments ($P < 0.05$; $F = 22.415$; Fig. 4). It (293.4 mg g^{-1}) was the highest in

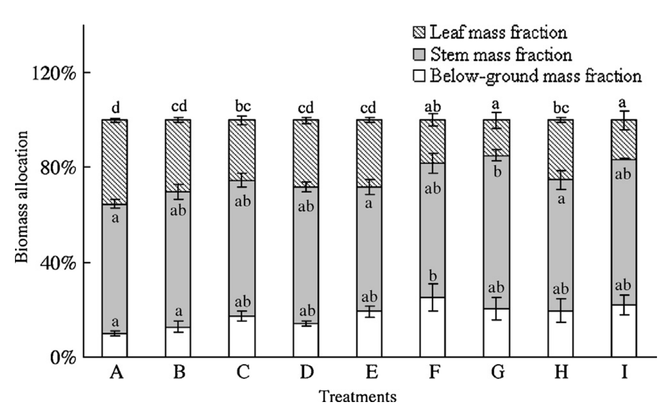

Fig. 3. Biomass allocation (means ± standard error (SE), $n = 3$) of *Polygonum hydropiper* grown at three densities under three water levels. Different letters indicate significant differences among treatments at the 0.05 significance level. Please refer to Fig. 1 for the meanings of the capital letters.

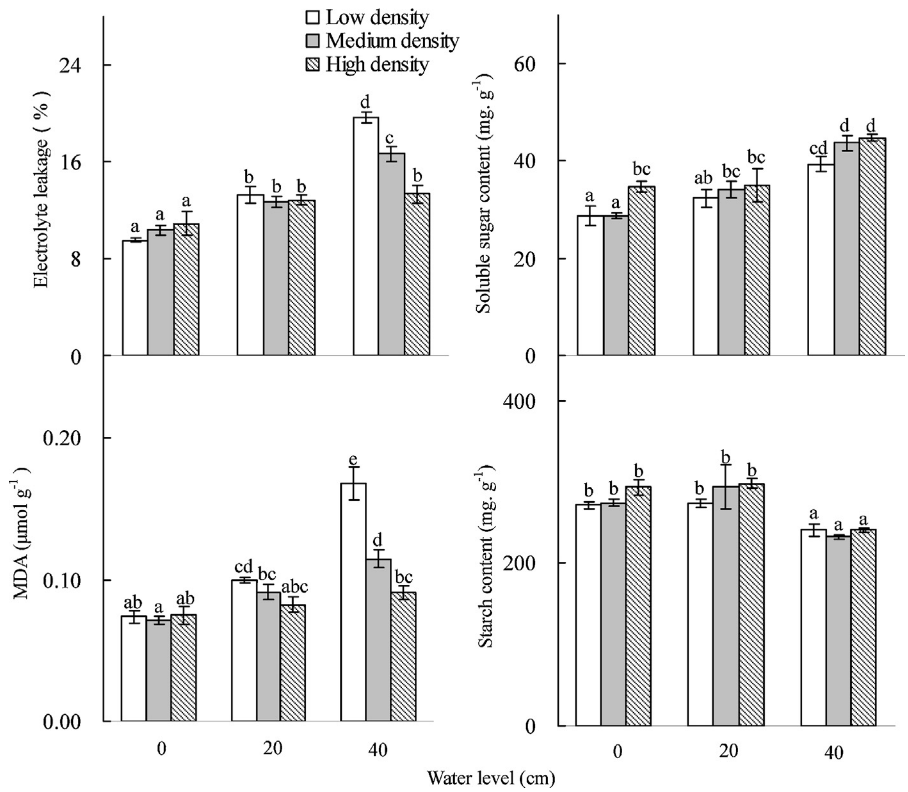

Fig. 4. Electrolyte leakage, malondialdehyde (MDA) content, soluble sugar content, and starch content (means ± standard error (SE), $n = 3$) of *Polygonum hydropiper* grown at three densities under three water levels. Different letters indicate significant differences among treatments at the 0.05 significance level.

the 0 cm water level + high-density treatment and was 1.26 times higher than the lowest starch content (232.8 mg g^{-1}) in the −40 cm water level + medium-density treatment.

4. Discussion

Biomass accumulation was the highest at the −20 cm water level + low density treatment, suggesting that this depth provided the most suitable environment for plant growth. *P. hydropiper* is an annual plant species that can grow in either terrestrial or shallow-flooded habitats such as riverbanks, streamsides, and wet valleys (Griffith and Sultan, 2006; Li et al., 2003), and might therefore grow better in elevated areas than in shallow-flooded habitats where anoxic conditions are commonly prevalent. We also found that water level had no influence on the growth of *P. hydropiper* at medium and high densities, which is consistent with our first hypothesis. The positive influence of density might be explained by the more humid microenvironment found at higher densities, which is supported by our results for soil water content and by the findings of other studies (Tu, 1997; Asghari et al., 2009).

In our study, biomass allocation (except that of leaf mass fraction) was not significantly affected by water level or density, which contradicts our second hypothesis. Caloin et al. (1990) proposed that partitioning of assimilates between shoots and roots is controlled by genetic and environmental factors. Plants in Dongting Lake experience frequent drought stress, and this has been particularly so in recent years. Therefore, *P. hydropiper* might have adapted to drought stress, and hence the change in water availability in our experiment did not alter biomass allocation patterns.

MDA content and electrolyte leakage, important indicators of lipid peroxidation and membrane damage, are known to increase under drought conditions (Luo et al., 2008; Li et al., 2013). In this study, electrolyte leakage and MDA content increased considerably with decreasing water level in the low-density treatment compared with the medium- and high-density treatments. Increased MDA accumulation and electrolyte leakage might have been caused by increased membrane permeability or loss of membrane integrity (Masood et al., 2006; Li et al., 2013). These results are in agreement with our third hypothesis and confirm that drought damage to *P. hydropiper* was more severe at low density than at high density. Moreover, we found that MDA content and electrolyte leakage changed insignificantly at the 0- and −20 cm water levels, suggesting that density effects depend on water levels. Plant growth might not have been limited by water in these treatments, which could explain the similar patterns in MDA accumulation and electrolyte leakage.

The tolerance mechanism for water deficit might be associated with the accumulation of osmoprotectants such as proline and soluble sugars (Liu et al., 2011). Soluble sugars are known to play various complex and essential roles in plant metabolism; sugars, products of hydrolytic processes, serve as substrates in biosynthetic processes, energy production, and sugar-sensing and signaling systems (Hessini et al., 2009). In this study, higher soluble sugar content but lower starch content in the low-water level treatment indicated that an increase in soluble sugars through the inversion of some carbohydrates might contribute to enhanced desiccation tolerance and allow the maintenance of metabolic activity (Hoekstra and Buitink, 2001), which has been well documented in other studies (Liu et al., 2011).

In conclusion, our study confirmed that increased plant density could facilitate the acclimation of *P. hydropiper* to drought stress, and this might have been a result of higher soil water content in the higher density treatments. Therefore, this study provides experimental evidence that high density might facilitate plant acclimation to various environmental conditions (Retuerto et al., 1996; Luo et al., 2010). Moreover, in the vegetation restoration process, the water needed for plantations should be balanced with the soil water supply capacity. One possible way of maintaining soil water balance is by adjusting plant density. Therefore, our study might shed light on the important role of density in the restoration and stability maintenance of *P. hydropiper* communities.

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