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Negative influence of burial stress on plant growth was ameliorated by increased plant density in *Polygonum hydropiper*

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ABSTRACT

Sedimentation and density are important factors influencing the growth of wetland plants. The aim of this study was to elucidate the role of plant density in acclimation to burial stress by investigating the growth, biomass allocation, and carbohydrate contents of *Polygonum hydropiper* L. var. *flaccidum*, one of the dominant species in the Dongting Lake wetland, China. Experimental treatments, conducted in a greenhouse, combined three plant densities (16, 144, and 400 plants m^{-2}) with two burial depths (0 and 15 cm) in a factorial design. Greater burial depth and higher plant density had negative effects on biomass accumulation and plant height with some exceptions. Plant growth, although lower at higher densities in general, was unaffected by burial depth at medium and high densities, indicating that the negative effect of burial stress was ameliorated by increased plant density. Deeper burial led to higher stem mass fraction only in the low-density treatment. Belowground mass fraction increased significantly with increasing density in both burial treatments. Moreover, higher density and deeper burial led to higher soluble sugar content but lower starch content. These data indicate that higher density facilitates acclimation of *P. hydropiper* to burial stress through increased soluble sugar content.

Introduction

Sedimentation is a major limitation to plant survival and growth in wetland ecosystems, especially in coastal areas, river-connected lakes, and floodplains (Bai et al., 2012; Pan et al., 2012). Major stresses imposed by sedimentation include the reduction of oxygen concentration in the root zone and physical overburden on plant apical meristems (Maun, 1998; Chen et al., 2011). Generally, plants are able to tolerate a certain degree of sedimentation stress, especially those growing in habitats characterized by regular sediment accretion, some of which even require regular burial to maintain high vigor (Maun, 1998; Li and Xie, 2009). Functional responses of plants to burial include accelerated vertical growth achieved by elongation or increased numbers of stem internodes, increased allocation of energy to aboveground parts, and enhancement of soluble sugar content (Dech and Maun, 2006; Li and Xie, 2009; Pan et al., 2012). Additional responses to burial involve seeds and roots, including changes in seed mass and persistence, production of adventitious roots, generation of alcohol dehydrogenase, and increased root diameter (Kent et al., 2001; Langlois et al., 2001; Xiong et al., 2001; Pan et al., 2012). These adjustments help plants to grow out of the sediment or acclimate to the anaerobic environment to escape from sedimentation stress.

The role of intraspecific competition in maintaining vegetation structure and population dynamics has been extensively investigated (Cappuccino, 2004; Li et al., 2009). In a dense canopy, plant growth may be inhibited due to intense competition for limited resources (Shilo-Volin et al., 2005). However, in contrast to this negative influence, a dense canopy may help to ameliorate other environmental stresses (Retuerto et al., 1996; Franks and Peterson, 2003; Luo et al., 2010). For instance, high density facilitates acclimation of marsh plants to flooding stress by forming a relatively oxygen-rich environment (Luo et al., 2010). In drought conditions, evaporation under a dense canopy can be reduced by shading, which can then lead to higher survival rates of seedling (Bertness and Hacker, 1994). Physical and physiological effects of wind were ameliorated by higher density in *Sinapis alba* (Retuerto et al., 1996). Increasing attention is being paid to the positive effects of high plant density.

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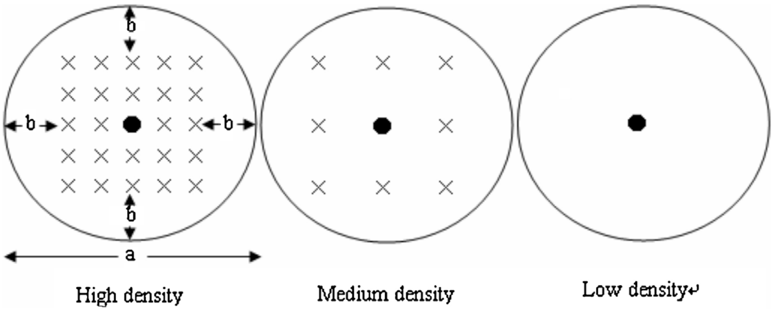

Fig. 1. Experimental design of the experiment. " × " means neighbor plants, "●" means target plants. $A = 30$ cm; $b = 2.5$ cm.

Plants can acclimate to a dense canopy by morphological and physiological adjustments such as reallocation of resources between shoots and roots, shifting from sexual to vegetative reproduction, increased photosynthesis rates, and elongation of stems through increasing length and number of internodes (Lentz, 1999; Li et al., 2009). These changes increase plants' ability to acquire resources (e.g., nutrients, light). For example, shoot:root ratio would be expected to decrease with increased density as plants shift more resources toward light-gathering structures (Lentz, 1999). An increase in allocation to vegetative reproduction under high density may increase competitive strength (Van Kleunen et al., 2001). The ways in which adjustments are made in response to density depend on the plant species and factors such as nutrient and light availability (Li et al., 2009). Higher plant density may facilitate acclimation to burial stress. For example, enhanced shoot:root ratio are beneficial in escaping from sedimentation.

Dongting Lake is the second-largest freshwater lake, and the most typical river-connected lake, in China. Sedimentation rate in the lake is approximately 3.7 cm year^{-1} during the flooding period and is an important driving force regulating community succession (Li et al., 2008; Xie and Chen, 2008). The objective of this study was to examine whether the negative influence of burial stress on plant growth can be ameliorated by increased plant density. Specifically, we tested the following hypotheses: (1) biomass accumulation and plant height will decrease with increasing burial depth and density, and the negative influence of burial will be ameliorated at higher plant density; (2) stem mass fraction and soluble sugar content will increase, but belowground mass fraction and starch content will decrease significantly with increased density, since these adjustments are beneficial for acclimation to burial stress. To this end, *Polygonum hydropiper* L. var. *flaccidum*, a dominant macrophyte in the Dongting Lake wetland, was grown in three densities and at two burial depths in a greenhouse experiment. Plant growth, biomass allocation patterns, and contents of soluble sugar and starch were examined.

Materials and methods

Study location and plant materials

P. hydropiper, an annual wetland macrophyte, is primarily found in mesic, moist, or wet habitats, such as riverbanks, streamsides, and wet valleys (Hobbs, 1992; Sultan, 2001). In the Dongting Lake wetland, *P. hydropiper* forms large monodominant patches or is a co-dominant with *Carex* species (Peng et al., 1984). This species flowers and fruits from April to May, before onset of the flooding season in the wetland, and recruits mainly through production of vegetative ramets from rhizomes (Hou et al., 2009; Chen et al., 2011). Ramets of *P. hydropiper* were collected in December 2011 from a monodominant stand in Chunfeng Village (29°13′49.72″N, 113°02′32.79″E), East Dongting Lake wetlands, China. The ramets were cut into 20 cm × 20 cm sections and transported to a greenhouse at the Institute of Subtropical Agriculture, the Chinese Academy of Sciences, Changsha, Hunan province. Additionally, 0–20 cm soil was collected from the same site. To germinate new ramets, plant fragments with roots were placed into plastic buckets containing 15 cm soil collected from the *P. hydropiper* community. The soil contained 1.87% organic matter, 28.5 μg g^{-1} total N and 7.83 μg g^{-1} total P. Temperature in the greenhouse was controlled at 25 ± 2 °C during the day and 17 ± 2 °C at night, and light was provided by 400-W SON-T ARGO sodium lamps (Philip Company, Guildford, UK) at a photon flux density of 600 μmol m^{-2} s^{-1} (PAR) and a 14-h photoperiod. 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) was supplied daily according to the plant growth.

Experimental set-up

The experiment combined two burial depths (0 and 15 cm) with three plant densities (low, 16 plants m^{-2}; medium, 144 plants m^{-2}, and high, 400 plants m^{-2}) in a factorial design with four replicates. The density treatments were selected according to the field investigation, where density ranged from 25 to 390 plants m^{-2}. The experiment included six treatments: two single-individual treatments (one plant per burial depth) and four multi-individual treatments (9 or 25 plants per burial depth, with the center individual designated as the target plant; Fig. 1). On 9 January 2012, 280 similar-sized ramets (6–7 leaves, approximately 23 cm in height) were cut from plant cultures and planted in PVC tubes (40 cm tall × 30 cm diameter) filled with 25 cm soil, the same soil used for plant incubation.

Six tubers (one per treatment) were placed into each of four large plastic bins (98 cm × 76 cm × 68 cm) to control water level. One-time burial was conducted after transplantation for one week. The sediment (0.76% organic matter, 7.5 μg g^{-1} total N, and 1.27 μg g^{-1} total P; soil particle composition including 72.4% sand, 21.9% silt, and 5.7% clay) used for burial treatment was collected from a beach in East Dongting Lake. Water depth was controlled at 25 cm during the experimental period; tap water was supplied as needed and was completely replaced every two weeks to prevent growth of algae.

Harvest

The plants were harvested after 100 days. Plant roots were carefully dug out by hand and cleaned with tap water. Plant height was measured using a 0.1-cm ruler, after which the plants were divided into leaves, shoots, and belowground parts (rhizomes and roots), oven dried at 80 °C for 48 h and weighed.

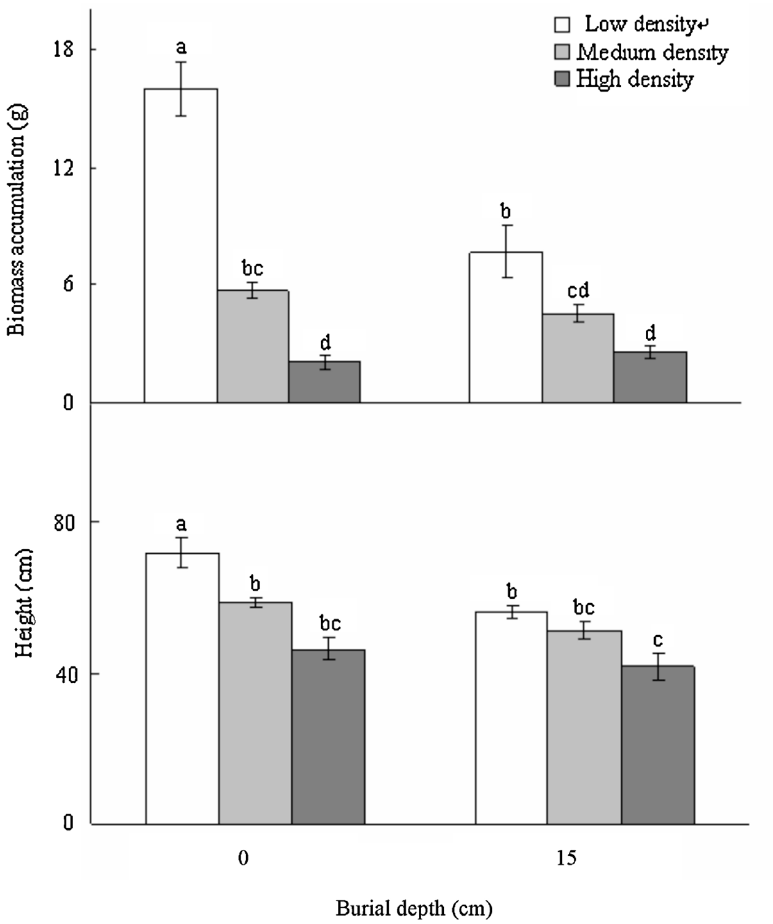

Fig. 2. Biomass accumulation and plant height (means ± SE, $n = 4$) of *Polygonum hydropiper* growing at three densities under two burial depths. Different letters indicate significant differences among treatments at the 0.05 significance level.

Carbohydrate analyses

Contents of soluble sugar and starch were analyzed according to the methodology described by Yemm and Willis (1954). Dry leaf samples were ground to fine powder and extracted three times using 80% ethanol (v/v). The extract was used for soluble sugar analysis after addition of anthrone reagent, followed by measurement of absorbance at 630 nm using a spectrophotometer (Beijing Puxitongyong Company, China). The residue that remained after extraction of soluble sugars was dried and extracted using 30% perchloric acid and analyzed for starch (as glucose equivalent) using the anthrone reagent.

Data analysis

Leaf, stem, and belowground mass fractions were determined as the ratios of each component to total biomass. Prior to analysis, bin effects on biomass accumulation, height, biomass allocation, and soluble sugar and starch contents were analyzed using Tukey's test at the 0.05 significance level. If bin effects were insignificant, two-way ANOVA was performed, with burial depth and plant density as main factors, to determine main effects and interactions for all the above indexes. Multiple comparisons of means were performed by Tukey's test and a Bonferroni correction for multiple comparisons 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 16.0 software for Windows (SPSS Inc., USA).

Results

Biomass accumulation and plant height

Burial depth ($P < 0.05$; $F = 19.149$), density ($P < 0.05$; $F = 68.258$), and their interactions ($P < 0.05$; $F = 15.852$) had a significant negative effect on biomass accumulation (Fig. 2). Biomass accumulation was highest (16.01 g plant^{-1}) in the 0-cm burial + low-density treatment and lowest (2.06 g plant^{-1}) in the 0-cm burial + high-density treatment. Moreover, biomass accumulation decreased significantly with increasing burial depth in the low-density treatments. Biomass accumulation was similar in the 0- and 15-cm burial + medium- and high-density treatments.

Plant height displayed a similar pattern as biomass accumulation, decreasing with increasing plant density ($P < 0.05$; $F = 24.107$) and burial depth ($P < 0.05$; $F = 15.876$) (Fig. 2). Compared to the 0-cm burial + low-density treatment, plant height decreased 21.9% in the 15-cm burial + low density treatment, while burial depth did not have a significant effect on plant height in the medium- and high-density treatments.

Biomass allocation

Stem and belowground mass fraction were significantly influenced only by plant density ($P < 0.05$; Fig. 3); higher plant density led to lower stem mass fraction in the 15-cm burial treatment, while belowground mass fraction increased significantly along with increasing plant density in both the 0- and 15-cm burial

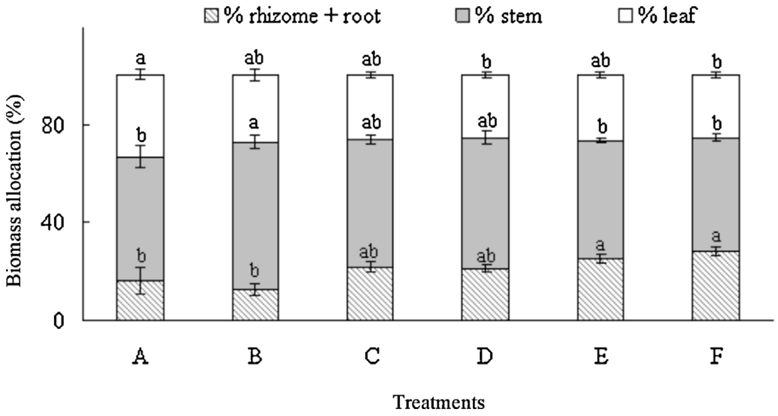

Fig. 3. Biomass allocation (means ± SE, $n = 4$) of *Polygonum hydropiper* growing at three densities under two burial depths. Different letters indicate significant differences among treatments at the 0.05 significance level. Treatment A: low density + 0-cm burial; Treatment B: low density + 15-cm burial; Treatment C: medium density + 0-cm burial; Treatment D: medium density + 15-cm burial; Treatment E: high density + 0-cm burial; Treatment F: high density + 15-cm burial.

treatments. Moreover, 15-cm burial led to a higher stem mass fraction only in the low-density treatments.

Contents of soluble sugar and starch

Soluble sugar content increased significantly with increasing plant density ($P < 0.05$; $F = 7.343$) and burial depth ($P < 0.05$; $F = 20.348$) (Fig. 4). Soluble sugar content was highest (27.4 mg g^{-1}) in the high-density + 15-cm burial treatment, which was 1.4 times higher than in the 0-cm burial + low-density treatment (19.9 mg g^{-1}).

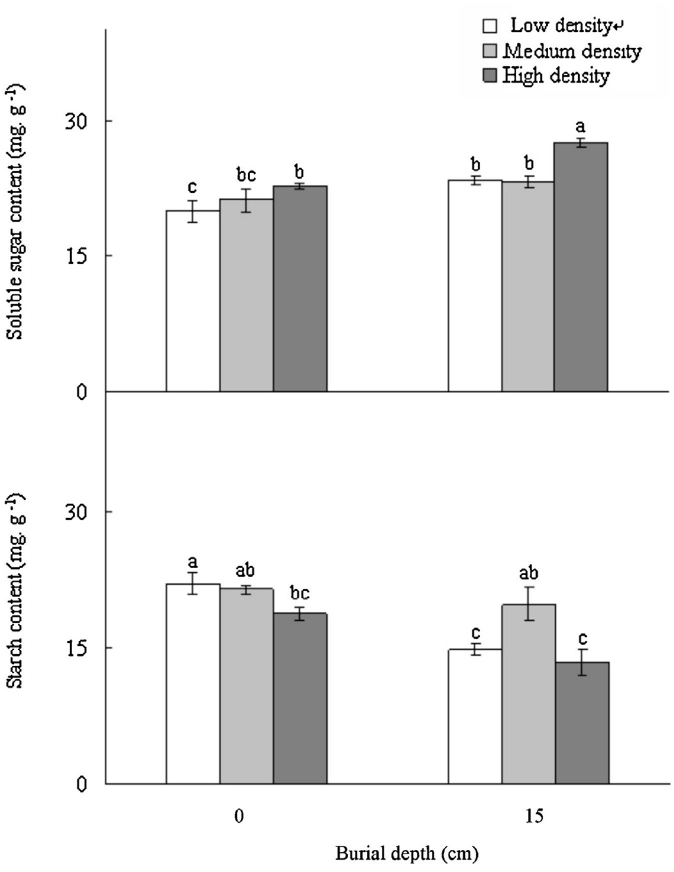

Fig. 4. Soluble sugar content (means ± SE, $n = 4$) and starch content (means ± SE, $n = 4$) of *Polygonum hydropiper* growing at three densities under two burial depths. Different letters indicate significant differences among treatments at the 0.05 significance level.

Starch content displayed the opposite pattern as soluble sugar content, decreasing with increasing plant density ($P < 0.05$; $F = 6.857$) and burial depth ($P < 0.05$; $F = 8.339$) (Fig. 4). Starch content was highest (22.1 mg g^{-1}) in the 0-cm burial + low-density treatment and lowest (13.4 mg g^{-1}) in the high-density + 15-cm burial treatment.

Discussion

In this experiment, biomass accumulation and height of *P. hydropiper* were reduced significantly by 15-cm burial at low plant density. These results agree with our first hypothesis. The negative influence of sedimentation on plant growth has been widely reported in other studies (Pan et al., 2012), and might be explained by its effects on a variety of physical factors in the soil-plant microenvironment such as aeration, temperature, and pH (Maun, 1998; Lowe et al., 2010).

The influence of density on plant growth has been extensively investigated (Cappuccino, 2004; Shilo-Volin et al., 2005). When population density is low, intraspecific facilitation may be important. When density is high, there is strong intraspecific competition, which reduces plant growth and causes mortality (Li et al., 2009). In comparison to the low-density treatment, lower biomass accumulation and plant height in the other two density treatments suggested that plant growth was strongly inhibited by high density, which might have been a result of lower resource availability (Driever et al., 2005; Zhou et al., 2012).

Our study also confirmed that the negative influence of burial was ameliorated by higher plant density, reflected by similar growth performance at 0- and 15-cm burial in the medium- and high-density treatments. This result is consistent with our first hypothesis and provides experimental evidence that high density can facilitate plant acclimation to environmental conditions such as flooding-induced stress. The positive influence might be a result of a relatively favorable microenvironment created by higher density (Bertness and Hacker, 1994; Luo et al., 2010). It is possible that high densities of *P. hydropiper* can alleviate soil anoxia by releasing oxygen into the soil from its well-developed aerenchyma (Qin et al., 2010), in which case plants would help to protect one another from burial stress. High density would also protect plants from the weight of the sediment after burial. The added soil may have been less compacted in the higher plant-density treatment, allowing buried plants to grow more easily due to better porosity in the root zone (Maun, 1998).

As a response to sedimentation, plants usually allocate more biomass to aboveground parts to facilitate their growth out of the sediment (Dech and Maun, 2006). In our experiment, higher stem mass fraction observed in the 15-cm burial treatment at low plant density, compared to that in the 0-cm treatment, suggested that enhancement of stem mass fraction is an effective way for *P. hydropiper* to acclimate to sedimentation stress. However, biomass allocation was not significantly influenced by burial at medium and high plant density, and belowground mass ratio increased significantly with increased plant density. These results indicated that acclimating to sedimentation by decreasing belowground growth was limited in higher-density treatments. This result disagreed with our second hypothesis. Actually, at high plant densities, patterns of biomass allocation may depend upon the resource that is in the most demand (Lentz, 1999). If light were most limiting, aboveground biomass (e.g., stems and leaves) would be expected to increase with increasing density as plants should shift more resources toward light-gathering structures. In contrast, belowground biomass would be expected to increase under conditions of nutrient limitation (Lentz, 1999; Li et al., 2009). Our results indicated that belowground competition was more important than aboveground competition in *P. hydropiper*, possibly because growth of this species was not limited by shading by neighboring plants. An increase in belowground mass fraction has been found in many other species in response to intraspecific competition (Lentz, 1999; Li et al., 2009).

Higher soluble sugar content and lower starch content in higher-density treatments suggested that starch can be transformed into soluble sugar to satisfy the energy requirements of physiological activity, which would help *P. hydropiper* acclimate to intraspecific competition and counteract burial stress by supplying energy to maintain anaerobic respiration (Pan et al., 2012). Enhancement of soluble sugar content has been confirmed as an effective way for *Carex brevicuspis*, another dominant species in the Dongting Lake with similar distribution patterns to *P. hydropiper*, to counteract burial stress (Pan et al., 2012).

In conclusion, our study confirmed that both high density and burial stress significantly reduced the growth of *P. hydropiper* and that the negative influence of burial stress on growth of this species was ameliorated by increased plant density. This positive influence of plant density resulted from enhanced soluble sugar content rather than from changes in biomass allocation under high plant density. In the Dongting Lake wetland, the *P. hydropiper* community has declined dramatically in recent years. Our study may shed light on the important role of density in maintaining the stability of the *P. hydropiper* community.

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