



Morphological and physiological responses to burial depth and sediment type in the wetland macrophyte *Miscanthus sacchariflorus*

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With 5 figures

Abstract: The aim of this study is to elucidate how the wetland macrophyte *Miscanthus sacchariflorus* acclimatizes to sedimentation by investigating growth, morphology and nutrient content in a five month greenhouse experiment under five treatments: no burial, 6 cm sand, 6 cm clay, 12 cm sand and 12 cm clay (using one time burial). Compared to no burial treatment, biomass accumulation decreased only in the 12 cm sand burial treatment (9.5 versus 13.7 g plant⁻¹). As depth of burial increased under both the sand and clay treatments, stem and leaf mass ratios, root diameter and P content in stems increased but root mass ratio and root length decreased. At 6 cm deep root mass ratio, mean root length and specific root length (SRL) were higher, while leaf and stem mass ratios, root diameter, P content in stems and N content in roots and leaves were lower in the sand than in the clay burial treatments. At 12 cm deep, only root mass ratio was higher, while stem mass ratio, N and P contents in roots were lower in the sand than in the clay burial treatments. This data indicates that the growth of *M. sacchariflorus* is not influenced by shallow burial through adjustments of biomass allocation and root morphology, and that clay facilitates *M. sacchariflorus* in acclimatizing to deep burial due to sufficient nutrient supply.

Key words: *Miscanthus sacchariflorus*, sedimentation, biomass allocation, nutrient, root morphology.

Introduction

Plants in coastal and lake-shore dune systems have a high risk of being buried by sediment due to water-level fluctuation, which has been recognized as an important limitation for the survival and growth of wetland macrophytes (Sun et al. 2010, Maun & Perumal 1999). Deep burial is usually inhibitory to plant growth for almost all species due to the reduction of oxygen availability in root zones (Maun 1998, Zhao et al. 2007). Moreover, the effect of sedimentation on plant growth varies with sediment type due to differing

nutrient availability (Deng et al. 2008, Li & Xie 2009). Currently much research has focused on the acclimatization of wetland plants to sedimentation intensity, whilst less attention has been paid to the interactive effects of sedimentation intensity and sediment type.

Under regular sediment accretion many wetland plants can withstand shallow burial through morphological and physiological adjustments (Maun 1998). As a response to sedimentation plants usually allocate more biomass to above-ground parts to enable growth out of the sediment surface, to acquire oxygen from the air (Dech & Maun 2006), and shift nutrients from

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roots to above-ground parts to maintain their photosynthetic capacity (Harris & Davy 1988, Brown 1997). Furthermore, plants develop short and thick roots with aerenchyma to facilitate the aeration of root systems under deep burial conditions (Maun et al. 1996, Chen & Maun 1999). However, a thick and short root is unfavorable for nutrient acquisition due to low root-soil contact (Eissenstat 1992, Wahl et al. 2001). Therefore, root characteristics favoring aeration might be disadvantageous for nutrient acquisition due to the trade off in optimal morphology to acclimatize to deep burial or infertile environments (Xie et al. 2009). However, it is unclear how wetland macrophytes adjust their morphology to cope with the dilemma in the environments with high sedimentation.

The interactive effect will be stronger than expected on the basis of both separate effects when the morphological adjustment of plant to acclimatize to one stress is prevented by another stress (Geiger & Servaites 1991). Therefore, infertile sediment might aggravate the damage of deep burial on plant growth, while the damage might be alleviated in the fertile sediment since more nutrients can be supplied for plant growth (Boedeltje et al. 2005, Deng et al. 2008). As a result, fertile sediment might be more favourable for counteracting the negative effects of deep burial than an infertile one.

Dongting Lake, the second largest freshwater lake and the most typical river-connected lake in China, is usually flooded from May to October, when a large amount of sediment is deposited annually (Zheng et al. 2009). The intensity of sedimentation is a major driving force regulating the succession model of vegetation in this wetland (Xie & Chen 2008). The objective of this study is to elucidate how the wetland macrophyte *Miscanthus sacchariflorus* acclimatizes to sedimentation, treated with three burial depths (0, 6 and 12 cm) and two sediment types (clay and sand) in a factorial design. *M. sacchariflorus*, an emergent macrophyte, is one of the dominant macrophytes in the Dongting Lake wetlands. This plant is one of the raw papermaking materials in China; owing to its fast growing cycle, high biomass production, short cooking time and easy pulping (Cappelletto et al. 2000). Here, the following hypotheses were tested: Firstly, biomass accumulation of *M. sacchariflorus* will decrease with increasing burial depth and will decrease more in the sand than in the clay treatments. Secondly, the ratio of shoot mass to total biomass and root diameter will increase but root length will decrease with increasing burial depth, with these changes being more obvious in the clay than in the sand treatments. Thirdly, nutrient content in roots

will decrease along with increasing burial depth, and nutrient content will be lower in the infertile sand than in the fertile clay treatments.

Material and methods

Plant materials

Ramets of *M. sacchariflorus* (with roots) were collected from a single population in the Chunfeng Village (N: 29° 13' 49.72"; E: 113° 02' 32.79"), East Dongting Lake, China, in June 2010. After collection, plants were transported to a greenhouse where the temperature was kept at $25 \pm 2^\circ\text{C}$ during the day and $17 \pm 2^\circ\text{C}$ at night, and the light was provided by 400 watt SON-T ARGO sodium lamps at a photon flux density of $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ (PAR) in a 14 h light/10 h dark cycle. The ramets were then planted into plastic buckets (88 cm \times 67 cm \times 63 cm), which contained 15 cm clay (18.6 g kg^{-1} organic matter, 28.5 $\mu\text{g g}^{-1}$ exchangeable N, 18.7 $\mu\text{g g}^{-1}$ exchangeable P, 1.12 g cm^{-3} bulk density, soil particle composition including 15.3% sand, 60.5% silt and 24.2% clay) excavated from the community of *M. sacchariflorus* in the Junshan, East Dongting Lake, to germinate new ramets.

Experimental design

The experiment was started on 18 July, 2010. A total of 30 ramets of a similar size (6–8 leaves, about 30 cm in height) were transplanted individually in PVC tubes (20 cm in height, 15 cm in diameter, one ramet per tube). In each tube 4 drainage holes (0.5 cm in diameter) were drilled evenly 6 cm above the tube bottom. Each tube was filled with 6 cm of clay (the same soil used for plant incubation).

A two-way factorial design was implemented, combining three burial depths (0, 6 and 12 cm) with two sediment types (sand and clay). A total of five treatments were included: no burial, 6 cm sand, 6 cm clay, 12 cm sand and 12 cm clay. Both 0 cm sand and 0 cm clay were combined into one treatment. Each treatment was replicated 6 times. All tubes were placed into six plastic buckets (76 cm \times 55 cm \times 45 cm, five tubes per bucket, one tube per treatment). One-time burial was initiated after plant transplantation for one week. The clay used for burial was the same as the soil used for plant incubation. The sand (7.7 g kg^{-1} organic matter, 16.5 $\mu\text{g g}^{-1}$ exchangeable N, 6.2 $\mu\text{g g}^{-1}$ exchangeable P, 1.33 g cm^{-3} bulk density, soil particle composition including 72.4% sand, 21.9% silt and 5.7% clay) was collected from a dock in the East Dongting Lake. Water depth was maintained at 6 cm with tap water (51.1 $\mu\text{g L}^{-1}$ $\text{NH}_4^+\text{-N}$, 176 $\mu\text{g L}^{-1}$ $\text{NO}_3^-\text{-N}$, 52.7 $\mu\text{g L}^{-1}$ $\text{PO}_4^{3-}\text{-P}$, pH=7.2) supplied as needed and completely replaced every two weeks.

Harvest and root morphology

The plants were harvested after five months. At harvest, the entire root system of each plant was carefully excavated and cleaned using tap water. The longest root and four representative full-grown adventitious roots (growing from rhizomes) were selected from each plant to measure the longest root length and mean root length using a Vernier caliper, respectively. "Full-grown" roots were defined as an adventitious root with maximum length (Bouma et al. 2001). Plants were then divided

into leaves, stems, rhizomes and roots. Fresh weight of about half of each plant tissue type was recorded, oven dried at 85 °C for 48 h, then reweighed to calculate a wet to dry conversion fraction for each tissue type. The remaining roots were used for the analysis of root morphology. Four adventitious roots from each plant were randomly chosen as a group to measure diameter, using a microscope with an ocular micrometer (Olympus BX51, Olympus, Japan). To measure specific root length (SRL), the length of four adventitious roots (cut off lateral roots), from each plant, were measured and total length calculated with fresh weight being recorded. SRL was calculated as the total root length divided by root mass. All root morphology data were averaged for statistical analysis on the basis of individual plant. Biomass accumulation was taken as the sum of root, rhizome, stem and leaf masses. Root mass ratio, rhizome mass ratio, stem mass ratio and leaf mass ratio were defined as the ratio of root, rhizome, stem and leaf mass to biomass accumulation, respectively.

Chemical analysis

Upon collection plant roots, rhizomes, stems and leaves were ground into powder. All samples were digested with H_2SO_4 - H_2O_2 , and analyzed for plant N and P concentrations using colorimetric analysis (Shi 1994). Three replicates were used for each treatment.

Statistical Analysis

All statistical analyses were performed using the software SPSS13.0 (SPSS Inc., USA). Two-way ANOVAs, with burial depth and sediment type as main factors, were performed to determine the main effects and interactions on biomass accumulation, biomass allocation, root morphology and plant P and N content. Multiple comparisons of means were performed by Duncan's test at the 0.05 significance level. Homogeneity was tested using Levene's test and dates were \log_{10} -transformed if necessary to reduce heterogeneity of variances.

Results

Biomass accumulation

Biomass accumulation was significantly affected by sediment type ($F=5.264$, %SS=10.9, $p < 0.05$), and the effect of burial depth on biomass accumulation was dependent on sediment type (with significant burial depth \times sediment type interaction, $F=5.613$, %SS=23.3, $p < 0.05$). Biomass accumulation was lower in the 12 cm sand burial treatment (9.5 g plant⁻¹, $p < 0.05$, Fig. 1), and was similar in the other four treatments (13.7–15.8 g plant⁻¹, $p > 0.05$, Fig. 1), indicating that deep sand burial (12 cm) inhibited the growth of *M. sacchariflorus*.

Biomass allocation

Along with increasing burial depth, root mass ratio decreased from 31.8% to 16.9% in the sand burial treat-

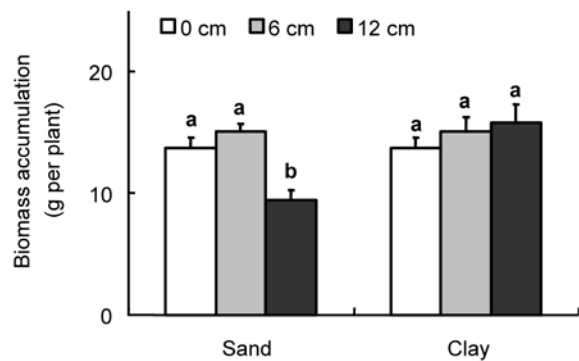


Fig. 1. Biomass accumulation of *Miscanthus sacchariflorus* ramets growing at three levels of burial depth and under two sediment types (mean \pm S.E., $n=6$). Different letters indicate significant differences among treatments. Multiple comparisons of means were performed by Duncan's test at the 0.05 significance level.

ments (or from 31.8% to 7% in the clay burial treatments). Stem mass ratio and leaf mass ratio increased from 21.5% to 33.7% and from 19.5% to 30.6% in the sand burial treatments (or from 21.5% to 48.0% and from 19.5% to 30.7% in the clay burial treatments) along with increasing burial depth ($p < 0.05$, Fig. 2). At 6 cm deep, root mass ratio was higher, but leaf and stem mass ratios were lower in the sand than in the clay burial treatments ($p < 0.05$, Fig. 2). At 12 cm deep in the sand burial treatment the root mass ratio was higher, but stem mass ratio was lower, than in the clay treatments ($p < 0.05$, Fig. 2). Root mass ratio and stem mass ratio were significantly affected by both burial depth ($p < 0.05$, Fig. 2) and sediment type ($p < 0.05$, Fig. 2), but only root mass ratio showed a significant burial depth \times sediment type interaction ($F=5.428$, %SS=6.3, $p < 0.05$).

Root characteristics

Root morphology was only affected by burial depth ($p < 0.01$). Roots were thickest at 12 cm clay burial (1.22 mm, $p < 0.05$, Fig. 3) but thinnest in the no burial treatment (0.62 cm, $p < 0.05$). Deeper burial (6 or 12 cm) usually led to a lower mean root length, the longest root and SRL ($p < 0.05$, Fig. 3). At 6 cm deep, mean root length and SRL were lower but root diameter was higher in the clay than in the sand burial treatments ($p < 0.05$, Fig. 3). However, root morphology showed no difference between the 12 cm clay and the 12 cm sand burial treatments. These results indicated that burial depth rather than sediment type was the primary factor in regulating root morphology.

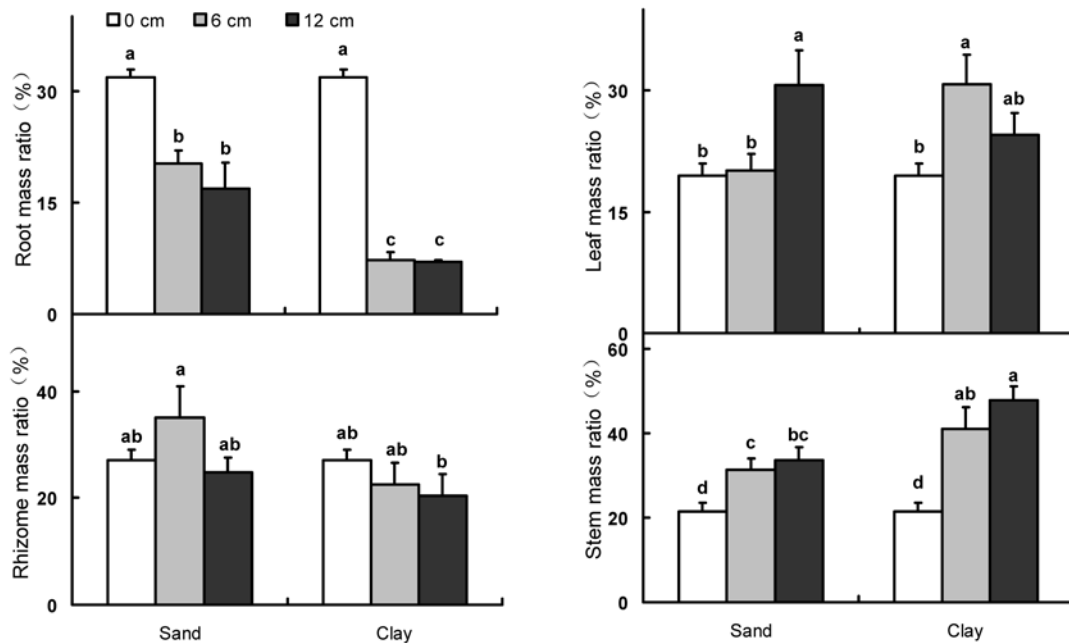


Fig. 2. Biomass allocation of *Miscanthus sacchariflorus* ramets growing at three levels of burial depth and under two sediment types (mean \pm S.E., $n=6$). Different letters indicate significant differences among treatments. Multiple comparisons of means were performed by Duncan's test at the 0.05 significance level.

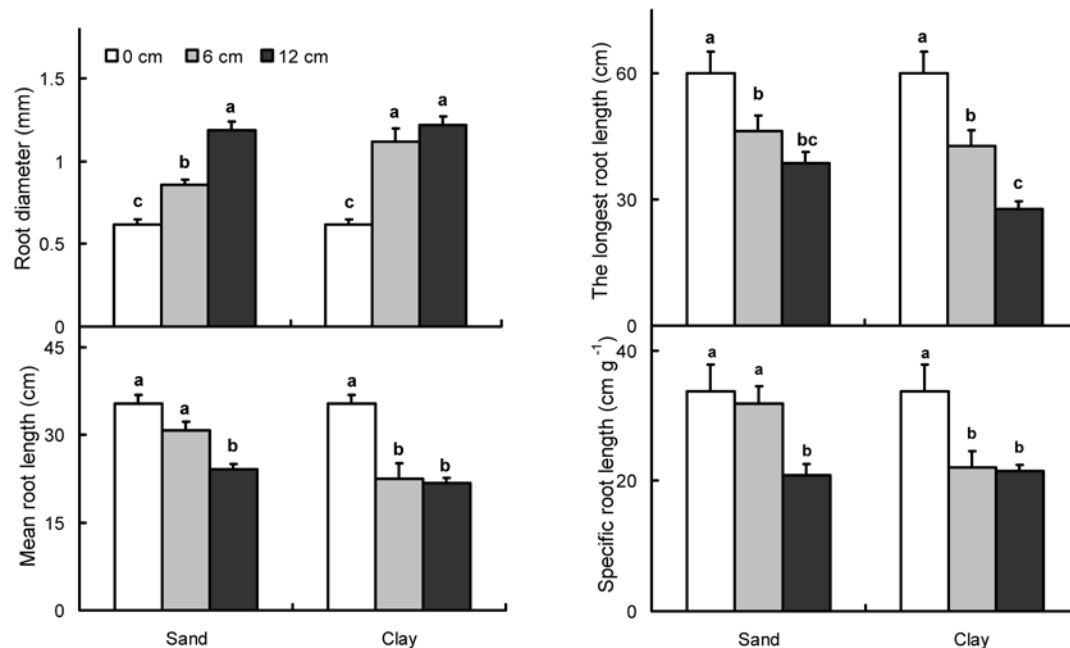


Fig. 3. Root diameter, mean root length, the longest root length and specific root length of *Miscanthus sacchariflorus* ramets growing at three levels of burial depth and under two sediment types (mean \pm S.E., $n=6$). Different letters indicate significant differences among treatments. Multiple comparisons of means were performed by Duncan's test at the 0.05 significance level.

Plant P and N contents

With increasing sand burial depth, P content decreased from 1.21 mg g⁻¹ to 0.85 mg g⁻¹ in roots and from 1.22 mg g⁻¹ to 0.99 mg g⁻¹ in rhizomes, but increased from 0.8 mg g⁻¹ to 1.02 mg g⁻¹ in stems ($p < 0.05$,

Fig. 4). However, P content in roots and rhizomes was unaffected by increasing clay burial depth ($p > 0.05$, Fig. 4). P content in roots was significantly affected by both burial depth ($F = 3.906$, %SS = 18.9, $p < 0.05$) and sediment type ($F = 12.958$, %SS = 32.0, $p < 0.01$), with

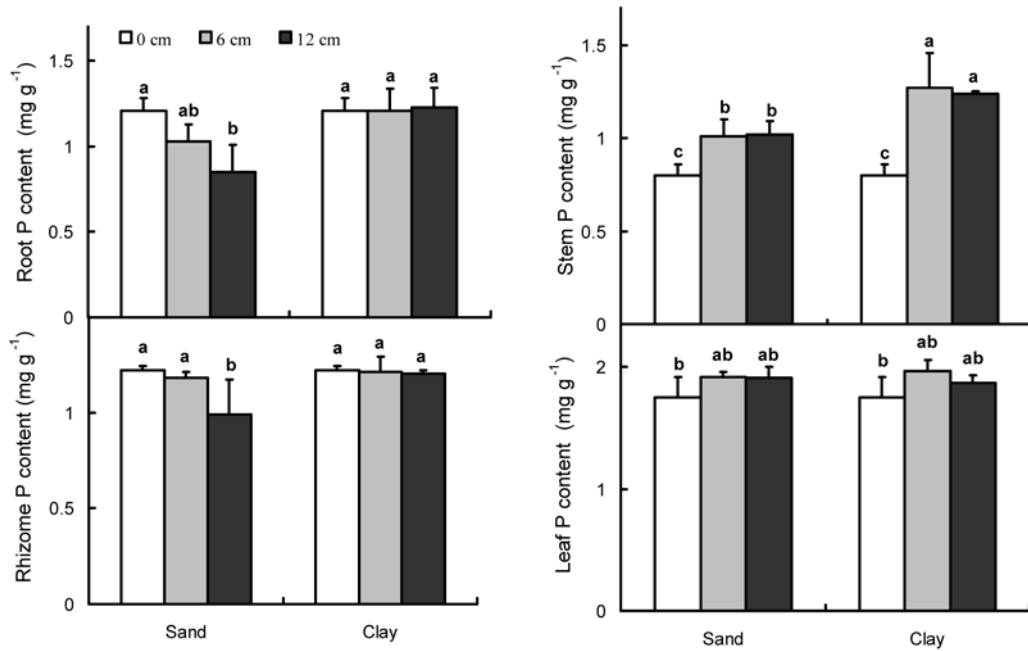


Fig. 4. Plant P concentration of *Miscanthus sacchariflorus* ramets growing at three levels of burial depth and under two sediment types (mean \pm S.E., $n = 3$). Different letters indicate significant differences among treatments. Multiple comparisons of means were performed by Duncan's test at the 0.05 significance level.

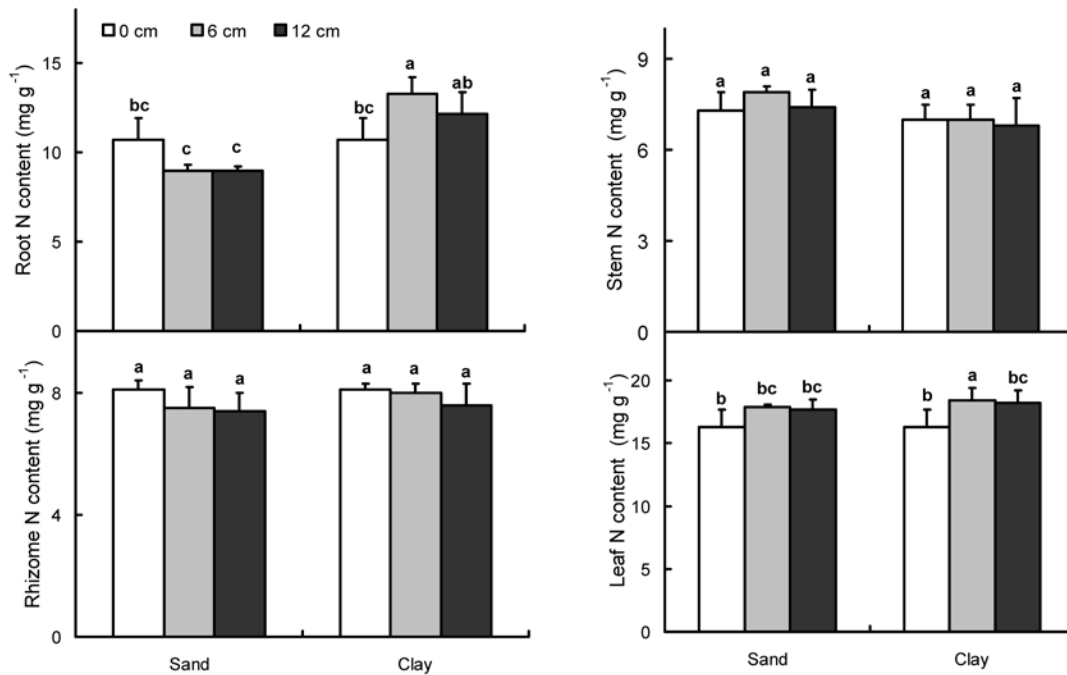


Fig. 5. Plant N concentration of *Miscanthus sacchariflorus* ramets growing at three levels of burial depth and under two sediment types (mean \pm S.E., $n = 3$). Different letters indicate significant differences among treatments. Multiple comparisons of means were performed by Duncan's test at the 0.05 significance level.

a significant burial depth \times sediment type interaction ($F = 4.345$, %SS = 20.8, $p < 0.05$). P content changed more dramatically than N content among the different

treatments (Figs 4 and 5). At the same burial depth (6 or 12 cm), N content in roots was lower in the sand than in the clay burial treatments ($p < 0.05$, Fig. 5).

Discussion

Lower biomass accumulation at 12 cm sand burial partly supported our hypothesis 1, which predicted that biomass accumulation of *M. sacchariflorus* would decrease along with increasing burial depth, with greater decreases in the sand than in the clay treatments. One of the reasons for this might be related to the infertile sand. Lower P content in roots and rhizomes indicates that nutrient deficiency is a major limitation for plant growth in the experiment (Gilbert et al. 2008), especially after plants have gained sufficient N nutrition (Woolmanse & Duncan 1980, Okada et al. 2004). In this study, mean root length and SRL decreased with increasing burial depth, but root diameter and leaf mass ratio was greater in the 12 cm sand burial than in the 6 cm sand burial treatments. Actually, short and thick roots and low root mass ratio are beneficial for plants to acclimatize to anoxic environments, but are disadvantageous for nutrient acquisition due to decreased root-sediment contact (Nielsen et al. 2001, Wahl et al. 2001). A low SRL is also unfavorable for nutrient acquisition since it increases the constructive cost for root formation (Eissenstat 1992). Therefore, nutrient deficiency might be a major limitation for the growth of *M. sacchariflorus* as a response to deep sand burial.

The acclimatization of wetland plants to sedimentation may rely on their biomass allocation and root morphology (Maun 1998, Sun et al. 2010). In this experiment less biomass was allocated to roots with increasing burial depth and only burial depth had significant influences on root morphology. These results are partly consistent with our hypothesis 2 on burial intensity. As a response to shallow sand burial (6 cm), more biomass of *M. sacchariflorus* was shifted from roots to stems; roots were comparatively shorter and thicker. These changes are favorable for plant acclimation to anoxic environments (such as flooding or sedimentation) by increasing oxygen transportation to root and/or by reducing the radial oxygen loss (Armstrong 1979, Visser et al. 1996, Colmer 2003). Many plants have similar root morphological responses to sedimentation (Maun et al. 1996, Chen & Maun 1999, Dech & Maun 2006). Additionally, plants usually produce new roots in the deposited sediment and/or form a shallow root system as a response to burial or anoxic environments, since oxygen is relatively higher in the top layer of soil (van der Putten et al. 1993, Lentz & Dunson 1998). Therefore, *M. sacchariflorus* can acclimatize to 6 cm sand burial through adjustments in biomass allocation and root morphology.

It was surprising that the effects of increasing clay burial depth on plant P content in roots were undetectable. This result partly contradicts our hypothesis 3, which predicted that nutrient content in roots would decrease along with increasing burial depth, and that nutrient content would be lower in the infertile sand than in the fertile clay treatments. This result is also inconsistent with some studies, reporting that many terrestrial and aquatic species tend to shift nutrients from below-ground to above-ground parts as a response to increasing burial depth (Harris & Davy 1988, Brown 1997). The mechanism might be related to the higher nutrient availability in the clay, as supported by the higher nutrient contents in both below and above-ground parts of plants. As a result, nutrients might not be the limiting factor for plant growth, and more resources can be used for acclimatization to hypoxia (Narsai et al. 2011). For example, root mass ratio was lower, but stem mass ratio was higher in the clay than in either the 6 cm or 12 cm sand burial treatments. Biomass accumulation was unaffected by increasing clay burial depth, indicating that fertile clay was favourable to counteract the negative effects of deep burial on the growth of *M. sacchariflorus* by adjusting biomass allocation pattern and root morphology. Xie et al. (2009) have also found that higher nutrient supply ameliorates the detrimental consequences of deep burial; facilitating development of root characteristics of *Deyeuxia angustifolia* to acclimatize to hypoxia. Therefore, high nutrient availability in the sediment plays an important role in acclimation to deep burial for *M. sacchariflorus*.

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