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Ability to acclimate to sedimentation gradually decreases with burial time in two emergent macrophytes from Dongting Lake wetlands in China

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Growth, below/above-ground mass ratio (BG:AG ratio), root morphology, carbohydrate content, and alcohol dehydrogenase (ADH) activity in the low-elevation species *Phalaris arundinacea* and the high-elevation species *Miscanthus sacchariflorus* buried under 0, 5, and 10 cm of sediment were investigated one, two, and three months after burial. Biomass accumulation, BG:AG ratio, and the starch content of both species generally decreased with increasing burial depth and burial time, except for higher biomass accumulation in *P. arundinacea* in the first month. In the first month, adventitious roots of both species, and first-order laterals of *P. arundinacea*, were shorter and thicker in the buried plants than in the controls. The ADH activity in both species and the soluble sugar content of *P. arundinacea* increased with increasing burial depth in the first month. Only the diameter of adventitious roots and the soluble sugar content of *P. arundinacea* were affected by burial depth after two or three months. It is concluded that *P. arundinacea* is more tolerant to sedimentation than *M. sacchariflorus* due to more efficient acclimation strategies in root morphology and soluble sugar content. However, the ability to acclimate becomes weaker over time due to consistently decreasing starch content and the trade-off between tolerance to sedimentation and plant growth.

Introduction

Sedimentation, a recurrent event in coastal and freshwater ecosystems, has far-reaching effects on plant growth and vegetation distribution (Maun 1994). These effects are mainly due to changes in soil aeration, soil redox potential, soil nutrient status, soil bulk density, and microorganism com-

position (Maun 1998, Zhao *et al*. 2007). Wetland plants differ considerably in their susceptibility to sedimentation (Shi *et al*. 2004, Sun *et al*. 2010). Because sediments can be an important source of nutrients and can reduce water evaporation (Walls *et al*. 2005, Zheng *et al*. 2012), short-term and relatively shallow burial may stimulate the growth of sedimentation-tolerant species due to increased nutrient or water availability in root zones. However, burial in sediment inhibits growth of sensitive species (Zhao *et al*. 2007, Pan *et al*. 2012), and even tolerant species are not able to withstand deep burial for extended periods (Shi *et al*. 2004, Li *et al*. 2010). Many studies have focused on the effects of burial depth on plant growth, while less attention has been paid to burial time. As a result, the effect of time on plant acclimation (morphological and physiological adjustments) to sedimentation is still unclear (Cabaço *et al*. 2008).

It is well known that sedimentation-tolerant species can withstand short-term burial through morphological and/or physiological adjustments, such as elongation of stems or leaves (Shi *et al*. 2004), lower root:shoot ratio (Dech & Maun 2006), shorter and thicker roots (Chen & Maun 1999), and higher alcohol dehydrogenase (ADH) activity and soluble sugar content (Sun *et al*. 2010, Pan *et al*. 2012). These mechanisms may be related to increases in oxygen transportation, decreases in oxygen loss from root tips, or a reduction in anoxic damage (Armstrong 1979, Colmer 2003). Parolin *et al*. (2002) found that low-elevation plants can tolerate longer periods of flooding and higher rates of sedimentation than high-elevation species. Therefore, low-elevation species might be more tolerant to sedimentation, and might have more efficient morphological and physiological strategies to acclimate to sedimentation. However, these responses are likely to vary over time (Bouma *et al*. 2001, Walls *et al*. 2005), because plants have to manage the supplies of critical resources to perform different functions (Bazzaz 1997). For example, long-term anaerobic metabolism in root tissues can lead to over-consumption of carbohydrates, which might decrease the carbohydrate available to support plant growth (Hook & Brown 1973). Additionally, plant roots that perform optimally after deep burial usually do not absorb nutrients due to the trade-off in optimal morphological acclimation to deep burial or nutrient absorption (Xie *et al*. 2007). Therefore, wetland plants may acclimate to short-term burial through morphological or physiological adjustment, but acclimation strategies likely become ineffective over time (Maun *et al*. 1996, Shi *et al*. 2004). This requires further confirmation.

Dongting Lake, the second largest freshwater lake and a typical river-connected lake in China, is periodically flooded from May to October, accompanied by heavy sedimentation (Li *et al*. 2008). In this study, we investigated the morphological and physiological adjustments of wetland macrophytes in response to different burial times. In a three-month greenhouse experiment, two wetland plants common in Dongting Lake were grown at three burial depths (0, 5, and 10 cm). The low-elevation species, *Phalaris arundinacea*, can grow on very low sandbars with heavy sedimentation, while the minimum altitude of the high-elevation species, *Miscanthus sacchariflorus*, is more than 1.5 m higher than that of *P. arundinacea* (Zheng *et al*. 2009). We tested three hypotheses: (1) biomass accumulation will decrease to a greater degree in *M. sacchariflorus* than in *P. arundinacea* after burial; (2) root diameter, soluble sugar content, and ADH activity will increase more and below/above-ground mass ratio (BG:AG ratio), root length and starch content will decrease more in buried *P. arundinacea* than in buried *M. sacchariflorus*; and (3) all these indices will gradually decrease over time and the decrease will be more pronounced in *M. sacchariflorus* than in *P. arundinacea*.

Material and methods

Plant material

On 13 April 2011, ramets of *P. arundinacea* and *M. sacchariflorus* were excavated from monodominant stands of the two species growing in Chunfeng Village (29°13´49.72´´N, 113°02´32.79´´E), East Dongting Lake, China. After collection, ramets were transported to a greenhouse at the Institute of Subtropical Agriculture, the Chinese Academy of Sciences, where the temperature was maintained at 25 ± 2 °C during the day and 17

± 2 °C at night. Light was provided by 400 watt SON-T ARGO sodium lamps at a photon flux density of 600 μmol m^{-2} s^{-1} (PAR) in a 14 h light/10 h dark cycle. The ramets were placed in plastic buckets (88 cm × 67 cm × 63 cm) containing 15 cm of soil (19 g kg^{-1} organic matter, 29 μg g^{-1} exchangeable N, 19 μg g^{-1} exchangeable P, 1.12 g cm^{-3} bulk density, and redox potential = 469 mV) that had also been excavated from Chunfeng Village in order to facilitate the development of new ramets.

Experimental design

On 21 May 2011, 36 ramets per species that were similar in size (2 or 3 leaves and 10 cm in height) were individually transplanted into 36 polyvinyl chloride (PVC) tubes (height 18 cm; diameter 11 cm; one ramet per tube). In each tube, four drainage holes (diameter 1 cm) were drilled at even intervals 6 cm above the bottom. Each tube was filled with 6 cm of the same soil (used for plant incubation). Prior to treatment, the morphological and physiological characteristics of three plants per species were measured. Previous study has shown that burial under 10 cm of sediment significantly inhibits the growth of *M. sacchariflorus* in the Dongting Lake wetlands, so 10 cm was chosen as the maximal depth (Pan *et al*. 2012).

A total of 72 tubes (36 tubes per species) were randomly assigned to one of four plastic buckets (88 cm × 67 cm × 63 cm, nine ramets per species per bucket). The tubes were randomly placed in each bucket. After one week, the plants were buried under 0, 5, or 10 cm of soil. The soil used for burial was the same as for plant incubation. The water depth in each bucket was maintained at 6 cm. Tap water (containing 51.1 μg l^{-1} NH_4^+-N, 176 μg l^{-1} NO_3^-N and 52.7 μg l^{-1} PO_4^{3+}-P, pH = 7.2) was supplied as needed and completely replaced every two weeks to prevent the growth of freshwater algae in the buckets.

Harvest and morphological measurement

For each burial depth, four plants per species (one plant per bucket) were harvested after one, two, or three months. After removal from the soil, the plants were carefully cleaned using tap water, divided into leaves, stems, rhizomes, and roots, and the fresh weight of each part was recorded (± 0.0001 g). Approximately half of the fresh roots of each plant were used for analysis of root morphology. The remaining plant tissues were dried in an oven at 85 °C for 48 h, and then reweighed to calculate the wet to dry conversion factor. Dry weights were then used for calculation. Biomass accumulation was calculated as the sum of the root, rhizome, stem, and leaf masses. The ratio of below-ground biomass to the above-ground biomass (BG:AG) was calculated as the ratio of root + rhizome biomass to stem + leaf biomass.

Root length and diameter were measured using a vernier caliper and a microscope equipped with an ocular micrometer (Olympus BX51; Olympus, Japan), respectively. Four representative full-grown adventitious roots and first-order laterals of maximum length (Bouma *et al*. 2001) from each plant were measured. The average root length and diameter for each plant was used in the statistical analyses.

Carbohydrate analyses

Non-structural carbohydrate content was analyzed according to the methodology described by Yemm and Willis (1954). Dry root samples were ground to fine powder and extracted three times using 80% ethanol (v/v). The extract was then used for soluble sugar analysis after addition of anthrone reagent, followed by measurement of absorbance at 630 nm using a spectrophotometer. The residue remaining after soluble sugars extraction was dried and extracted using 30% perchloric acid and analyzed for starch (as glucose equivalent) using the anthrone reagent.

ADH activity

The root system was separated from the plant and about 0.05 g of fresh root material was immediately placed in ice. ADH was extracted (4 °C) from powdered root tissue in 5 ml assay

mixtures (50 mM phosphate buffer pH 7.5, 5 mM $MgCl_2$,1 mM phenylmethyl sulfonyl fluoride). Plant extracts were then centrifuged at 15 000 rpm for 20 min at 4 °C. Finally, the ADH content in plant extracts was measured using diagnostic alcohol kits (Nanjing Jiancheng Bioengineering Institute, China). The results were expressed in enzyme units per milliliter of total serum protein; 1 U of the enzyme catalyzes the reduction of 1 nmol NAD+ per minute at a temperature of 37 °C.

Statistical analysis

Two-way ANOVA (followed by Tukey's test), with burial depth and treatment time as fixed factors, was used to determine their effects on biomass accumulation, BG:AG ratio, root length, root diameter, soluble sugar and starch content, and ADH activity. In case of first-order lateral-root diameter, Bonferroni correction for multiple comparisons was applied. Data were $\log_{10}$-transformed if necessary to meet the assumptions of normality and homoscedasticity. Normality was assessed using a kurtosis test, and homoscedasticity was tested using Levene's test. All statistical analyses were performed using the SPSS17.0 package (SPSS Inc., USA).

Results

Biomass accumulation

Biomass accumulation in both species was significantly affected by burial depth, and the effect of treatment time on biomass accumulation was dependent on burial depth (with significant burial depth × treatment time interaction, $p < 0.01$; Table 1, Fig. 1A and B). *Miscanthus sacchariflorus* did not survive three months buried under 5 cm of soil or two months buried under 10 cm of soil, but *P. arundinacea* survived the entire 3-month study period. In the first month, relative to that of the unburied plants, the biomass accumulation in *P. arundinacea* increased by 79.6% and 66.6%, while that of *M. sacchariflorus* decreased by 20% and 46.4% in the 5 and 10 cm burial, respectively. All the *P. arundina-*

Table 1. Summary of two-way ANOVA for biomass accumulation, below/above-ground mass ratio, adventitious root length, first-order lateral root length, adventitious root diameter, first-order lateral root diameter, starch content, soluble sugar content, and ADH activity in *Phalaris arundinacea* and *Miscanthus sacchariflorus* ramets growing under three burial depths at three harvest times.

			Burial depth (*B*)		Burial time (*T*)		*B* × *T*	
	Species	*n*	%SS	*p*	%SS	*p*	%SS	*p*
Biomass accumulation (g dry wt plant^{-1})	*Phalaris*	4	19.90	< 0.001	0.27	0.910	56.0	< 0.001
	Miscanthus	4	43.03	< 0.001	5.73	0.059	8.24	0.006
Below-:above-ground mass ratio	*Phalaris*	4	34.34	< 0.001	47.84	< 0.001	3.08	0.270
	Miscanthus	4	38.08	< 0.001	60.78	< 0.001	11.88	0.010
Adventitious root length (cm)	*Phalaris*	4	9.19	0.140	25.65	0.007	7.66	0.481
	Miscanthus	4	38.66	< 0.001	53.98	< 0.001	0.01	0.869
First-order lateral root length (cm)	*Phalaris*	4	27.23	< 0.001	29.09	< 0.001	12.58	0.053
	Miscanthus	4	1.57	0.854	5.23	0.421	8.74	0.313
Adventitious root diameter (μm)	*Phalaris*	4	38.08	< 0.001	23.92	0.001	6.43	0.276
	Miscanthus	4	63.00	< 0.001	11.33	0.052	0.03	0.976
First-order lateral root diameter (μm)	*Phalaris*	4	41.03	< 0.001*	3.77	0.277	17.63	0.030*
	Miscanthus	4	20.04	0.124	1.43	0.847	2.46	0.459
Starch content (mg g^{-1})	*Phalaris*	4	53.95	< 0.001	11.37	0.017	2.43	0.727
	Miscanthus	4	24.16	0.002	42.34	< 0.001	0.11	0.794
Soluble sugar content (mg g^{-1})	*Phalaris*	4	59.16	< 0.001	0.01	0.972	8.26	0.177
	Miscanthus	4	15.03	0.131	2.84	0.650	26.89	0.010
ADH activity (U ml^{-1} g^{-1} fresh wt)	*Phalaris*	4	51.93	< 0.001	7.86	0.008	22.14	< 0.001
	Miscanthus	4	42.52	0.001	19.71	0.018	6.73	0.079

* Bonferroni-corrected values

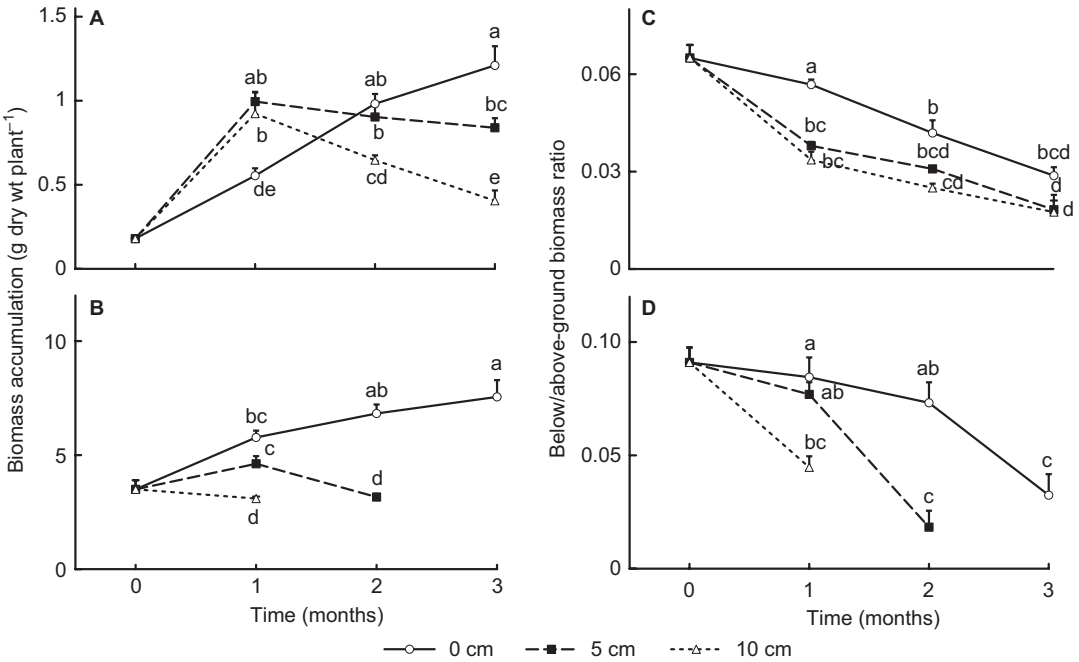

Fig. 1. (**A** and **B**) Biomass accumulation and (**C** and **D**) below/above-ground mass ratio in (**A** and **C**) *Phalaris arundinacea* and (**B** and **D**) *Miscanthus sacchariflorus* ramets growing under three burial depths (0, 5, and 10 cm) at three harvest times (one, two, and three months; means + SE, $n = 4$). Different letters indicate significant difference ($p < 0.05$) between treatments at each harvest time.

cea plants and most of the *M. sacchariflorus* plants (except one plant in the 10-cm-burial treatment) emerged from the sediment surface after one month. Subsequently, biomass accumulation decreased with increasing burial depth and burial time in both species.

Below/above-ground mass ratio (BG:AG ratio)

The BG:AG ratio in both species was significantly affected by burial depth and treatment time ($p < 0.001$; Fig. 1C–D), but only ratio in *M. sacchariflorus* it showed a significant burial depth × treatment time interaction ($p < 0.05$; Table 1 and Fig. 1D). As compared with that of the unburied plants, the BG:AG ratio in *P. arundinacea* decreased in both 5 and 10-cm-burial treatments during the first month by 33.2% and 40.8%, respectively, but that of *M. sacchariflorus* decreased only in the 10-cm-burial treatment by 47.1% ($p < 0.05$). After the first month, the BG:AG ratios in *P. arundinacea* and *M. sacchariflorus* decreased by 40.5% and 75.0% in the 10- and 5-cm-burial treatments relative to unburied plants after 2 months ($p < 0.05$), respectively. It is clear that the adjustability of the BG:AG ratio decreased gradually over time.

Root morphology

Root length was significantly affected by treatment time (Fig. 2), and root diameter was affected by burial depth in both species (Fig. 3), with the exception of the *M. sacchariflorus* first-order laterals, which were unaffected by either treatment time or burial depth ($p > 0.05$, Table 1). The effect of treatment time on the diameter of *P. arundinacea* first-order laterals was dependent on burial depth (with significant burial depth × treatment time interaction; $p < 0.05$, Fig. 3C). In the first month, the adventitious roots of both species, and first-order laterals of *P. arundinacea*, became shorter and/or thicker in the 5- and 10-cm-burial treatments as compared with those of the unburied plants. Subsequently, only in *P.*

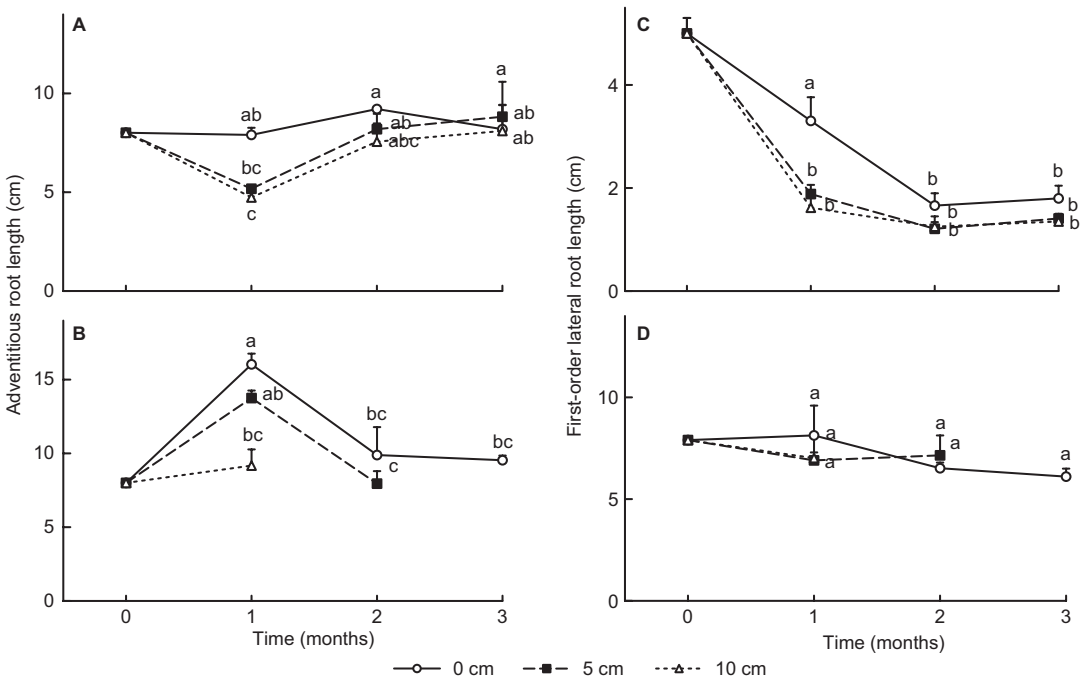

Fig. 2. (**A** and **B**) Length of adventitious roots and (**C** and **D**) first-order laterals of (**A** and **C**) *Phalaris arundinacea* (**B** and **D**) and *Miscanthus sacchariflorus* ramets growing under three burial depths (0, 5, and 10 cm) at three harvest times (one, two, and three months; means + SE, $n = 4$). Different letters indicate significant differences ($p < 0.05$) between treatments at each harvest time.

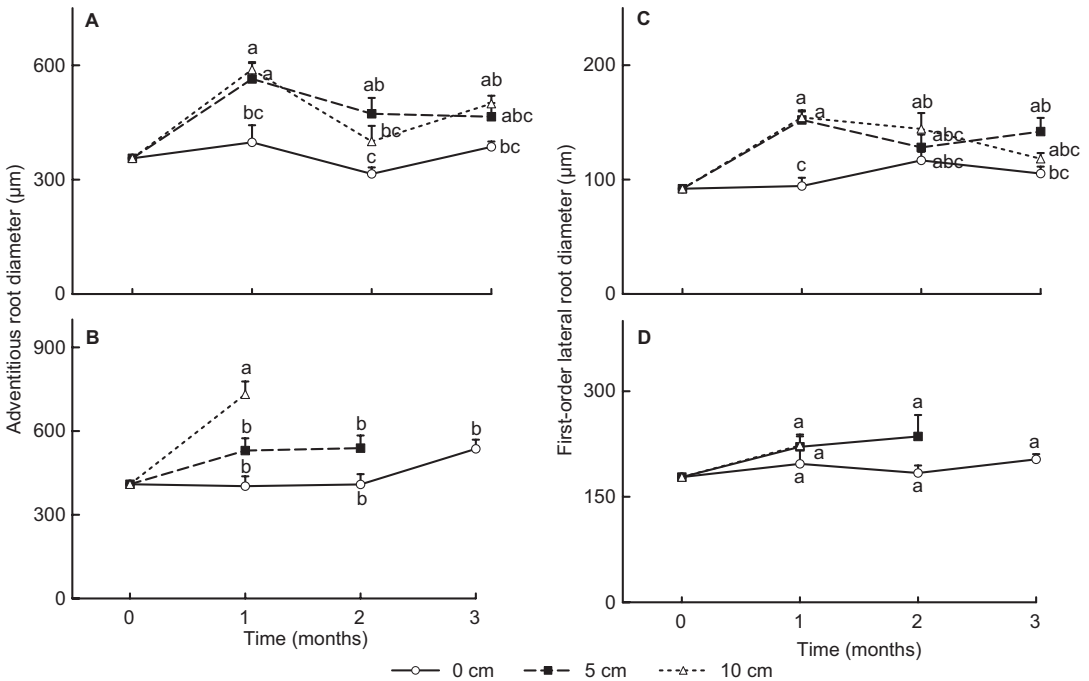

Fig. 3. (**A** and **B**) Diameter of adventitious roots and (**C** and **D**) first-order laterals of (**A** and **C**) *Phalaris arundinacea* and (**B** and **D**) *Miscanthus sacchariflorus* ramets growing under three burial depths (0, 5, and 10 cm) at three harvest times (one, two, and three months; means + SE, $n = 4$). Different letters indicate significant differences ($p < 0.05$) between treatments at each harvest time.

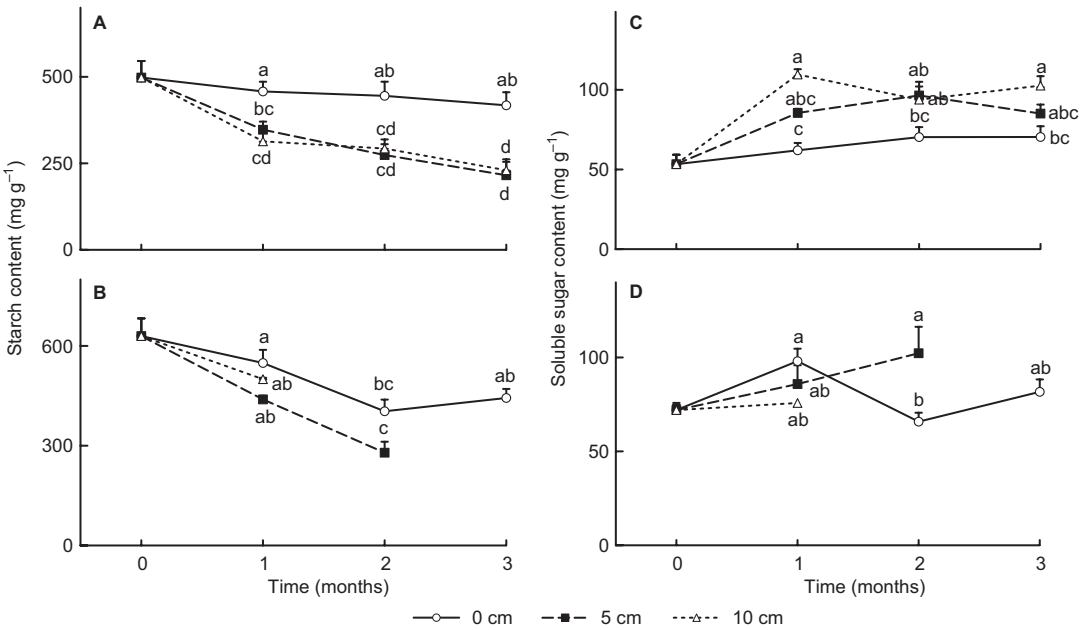

Fig. 4. (**A** and **B**) Starch content and (**C** and **D**) soluble sugar content in (**A** and **C**) *Phalaris arundinacea* and (**B** and **D**) *Miscanthus sacchariflorus* ramets growing under three burial depths (0, 5, and 10 cm) at three harvest times (one, two, and three months; means + SE, $n = 4$). Different letters indicate significant differences ($p < 0.05$) between treatments at each harvest time.

arundinacea the adventitious root diameter was affected by burial depth, increasing by 50.1% in the 5-cm-burial treatment after two months (Fig. 3A; $p < 0.05$). Therefore, root morphology responses to burial were more pronounced in the first month than in the subsequent two and three months.

Soluble sugar and starch contents

The starch content in both species was significantly affected by treatment time and burial depth ($p < 0.05$; Fig. 4A and B), while the soluble sugar content was only affected by burial depth in *P. arundinacea* ($p < 0.001$; Table 1, Fig. 4C). In the first month, the soluble sugar content in *P. arundinacea* increased by 76.7% relative to that in the unburied plants in the 10 cm burial, and the starch content in this species decreased by 24.3% and 31.5% relative to that in the unburied plants in the 5- and 10-cm-burial treatments. Subsequently, the soluble sugar content increased in both *P. arundinacea* (46% relative to that in the unburied plants in the 10 cm burial after three months) and *M. sacchariflorus* (55.3% relative to that in the unburied plants in the 5 cm burial after two months), but the starch contents decreased only in *P. arundinacea*: by 38.4% and 34.2% relative to that in the unburied plants after two months and by 46% and 44.9% relative to that in the unburied plants after three months in the 5- and 10-cm-burial treatments ($p < 0.05$), respectively. Therefore, the changes in carbohydrate content after sedimentation were species-specific.

ADH activity

The ADH activity in both species was significantly affected by burial depth and treatment time ($p < 0.05$; Fig. 5A and B), but only *P. arundinacea* showed a significant interaction between treatment time and burial depth ($p < 0.001$; Table 1 and Fig. 5A). As compared with the controls, the ADH activity in *P. arundinacea* (221%) increased more than that in *M. sacchariflorus* (162%) in the first month of the 10-cm-burial treatment. Subsequently, only the ADH

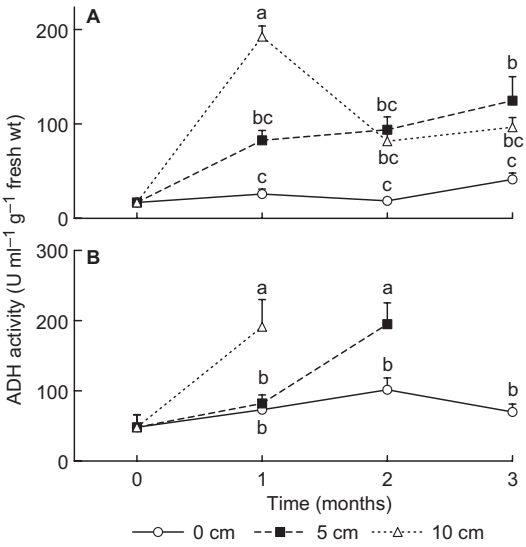

Fig. 5. ADH activity in (**A**) *Phalaris arundinacea* and (**B**) *Miscanthus sacchariflorus* ramets growing under three burial depths (0, 5 and 10 cm) at three harvest times (one, two, and three months; means + SE, $n = 4$). Different letters indicate significant differences ($p < 0.05$) between treatments at each harvest time.

activity in *M. sacchariflorus* increased (138% relative to that in the controls in the 5-cm-burial treatment) after 2 months ($p < 0.05$).

Discussion

In the first month, burial (5 or 10 cm) inhibited the growth of the high-elevation species, *M. sacchariflorus*, but stimulated the growth of the low-elevation species, *P. arundinacea*. Ramets of *M. sacchariflorus* died after two or three months, while those of *P. arundinacea* did not. These results directly support our first hypothesis: biomass accumulation will decrease to a greater degree in *M. sacchariflorus* than in *P. arundinacea*. In this study, the low-elevation species was more tolerant to sedimentation than the high-elevation species, and this result is consistent with those of other studies (Parolin *et al.* 2002, Pan *et al.* 2012). Acclimation ability may be related to morphological and physiological adjustments to sedimentation (Maun 1998).

The main factor associated with sedimentation that affected the growth of both species may be decreasing oxygen availability in the root zones (Ferreira *et al.* 2009). This was confirmed by increases in ADH activity with burial depth in both species in the first month. ADH activity is usually considered to be a direct indicator of oxygen deficiency in plant roots (Chen *et al.* 2005). Low oxygen availability resulted in shorter and thicker adventitious roots and lower BG:AG ratios in both species after the first month, as these strategies are beneficial for the acclimation of plants to anoxia (Maun *et al.* 1996, Dech & Maun 2006). However, the two species tested differed in their responses, indicating differences in the degree of anoxia tolerance. For example, in the first month, only *P. arundinacea* responded to deep burial by growing thicker and shorter first-order laterals and increasing soluble sugar contents. The lateral root systems of most anoxia-sensitive species are not able to effectively acclimatize toward anaerobiosis, and are very susceptible to long-term anoxia (Blom & Voesenek 1996). The decreased lateral root length of anoxia-tolerant species in anoxic environments has also been found in other wetland species (Visser *et al.* 1997). Moreover, high soluble sugar content may be indicative of the ability to supply sufficient energy for maintenance of anaerobic respiration (Li *et al.* 2007). It is clear that the morphological and physiological strategies employed by *P. arundinacea* for burial acclimatization were more efficient than those employed by *M. sacchariflorus*, which partly supports our second hypothesis: after burial, there will be a greater increase in root diameter and soluble sugar content as well as in root length in *P. arundinacea* than in *M. sacchariflorus*.

Treatment time negatively affected the growth of both species under deep burial conditions, but only *P. arundinacea* showed an interaction between treatment time and burial depth, as ramets of *M. sacchariflorus* were unable to withstand long-term burial. The effects of sedimentation on plant growth reported in the literature are complicated. For example, after a certain length of time, some buried plants start to recover, catch up, and then surpass plants that were not buried (Zhang & Maun 1990, Sykes & Wilson 1990), whereas other plants continuously decline as burial time increases (Maun 1998). In addition to

the complex results associated with burial depth and species characteristics (Sun *et al*. 2010, Pan *et al*. 2012), another difficulty arises because the effects of treatment time are generally ignored in most studies. However, because wetland species can usually survive months of anaerobic stress, acclimation responses may be a dynamic adjustment to anoxia (Xie *et al*. 2008, Zheng *et al*. 2009), as shown by the present study.

In our experiment, long-term (3-month) burial did not lead to ADH activity or soluble sugar content that were persistently greater than in the controls, nor did it lead to persistently thicker and shorter roots than in the controls, in either species. These results partly support our third hypothesis: the ability of plants to adjust to burial will gradually weaken over time. One of the reasons for this decrease in the ability to adjust to burial may be related to decreases in starch content with increasing burial time, as starch can be transformed into soluble sugar in order to satisfy the energy required for the necessary physiological and morphological adjustments (Chen *et al*. 2005). Another reason might be related to the trade-off between acclimation to environmental stresses and plant growth: plants invest energy in acclimatization to sedimentation at the expense of plant growth (Bazzaz 1997). Long-term limitation of the energy available for plant growth may result in negative feedback to the ability of wetland plants to acclimatize to sedimentation. For example, the BG:AG ratio in both species decreased dramatically with increasing burial depth and burial time. This decrease might help plants to acclimate to anoxia, but impedes the ability of roots to acquire nutrients (Barko *et al*. 1991, Wahl *et al*. 2001). As a result, roots became thinner and longer in order to increase root-sediment contact during the later stages of the experiment (Xie *et al*. 2007). Clearly, sedimentation-tolerant species can maintain high-vigor for a limited period of time after burial.

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