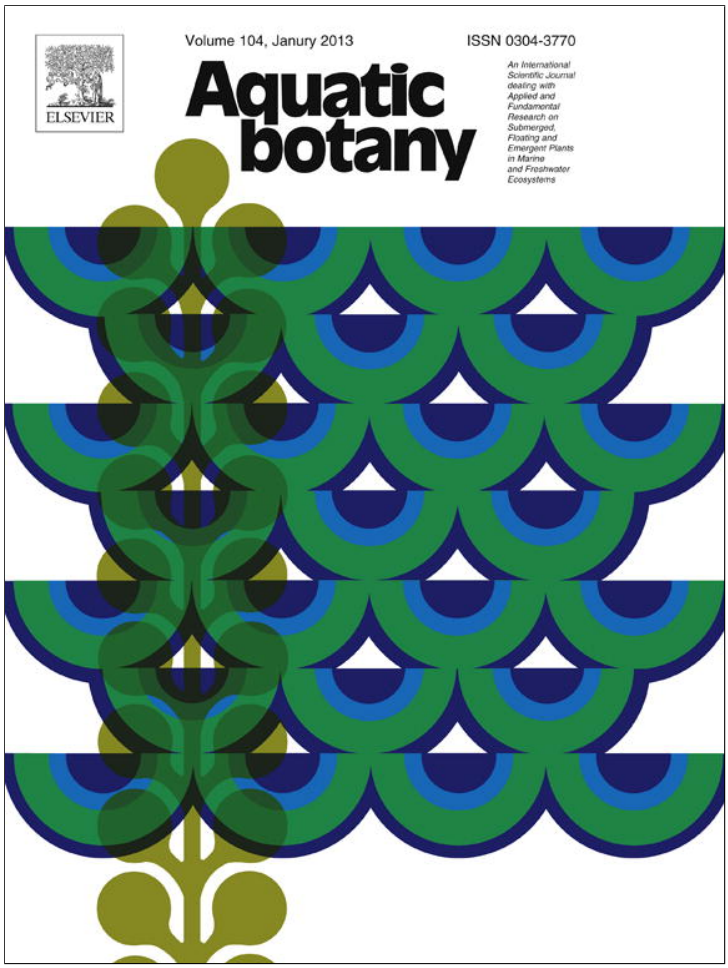

Aquatic Botany 104 (2013) 121–126

Contents lists available at SciVerse ScienceDirect

Aquatic Botany

journal homepage: www.elsevier.com/locate/aquabot

Effects of size and vertical distribution of buds on sprouting and plant growth of the clonal emergent macrophyte *Miscanthus sacchariflorus* (Poaceae)

Zhengmiao Deng[a,b,c], Xinsheng Chen[a,b], Yonghong Xie[a,b,*], Xu Li[a,b], Ying Pan[a,b,c], Feng Li[a,b]

[a] Key Laboratory of Agro-ecological Processes in Subtropical Region, Institute of Subtropical Agriculture, The Chinese Academy of Sciences, Hunan 410125, China
[b] Dongting Lake Station for Wetland Ecosystem Research, Institute of Subtropical Agriculture, The Chinese Academy of Sciences, Changsha 410125, China
[c] University of Chinese Academy of Sciences, Beijing 100049, China

ARTICLE INFO

Article history:
Received 18 June 2012
Received in revised form 20 August 2012
Accepted 20 August 2012
Available online 27 August 2012

Keywords:
Bud bank
Bud type
Plant regeneration
Soluble sugar

ABSTRACT

Sprouting from bud bank is important in plant regeneration to maintain population dynamics in clonal plants. The plant regeneration may be directly determined by the bud properties since buds are the primary shoot-producing meristematic organs. The aim of this study was to investigate sprouting and plant growth as affected by bud sizes (large and small) and vertical distribution in soil layer (0–10 cm and 10–20 cm) of the clonal emergent macrophyte *Miscanthus sacchariflorus* through a sprouting experiment. Sprouting ratio (*i.e.* the ratio of sprouted buds to total buds) was highest in large buds from the 0 to 10 cm soil layer (80%), intermediate in small buds from the 0 to 10 cm layer (70%) and in large buds from the 10 to 20 cm layer (60%), and lowest in small buds from the 10 to 20 cm layer (33.7%). Both plant height and accumulated biomass correlated with bud size, except for a higher accumulated biomass in small buds from 0 to 10 cm soil layer than those between 10 and 20 cm. The content of soluble sugar was highest in the large buds from the 0 to 10 cm soil layer (594.23 $\mu g\,g^{-1}$), and lowest in the small buds from the 10 to 20 cm layer (433.9 $\mu g\,g^{-1}$). Starch content was not affected by either bud size or soil layer. These data indicate that both bud size and distribution soil layer have significant effects on sprouting capacity and plant growth, which might be closely related to soluble sugar content in buds.

1. Introduction

The crucial role of regeneration from bud bank to maintain population dynamics, especially after severe disturbance, has been documented in different ecosystems (Klimešová and Klimeš, 2007), such as fire-prone areas (Choczynska and Johnson, 2009), arable lands (Klimešová and De Bello, 2009) and forest ecosystems (Bellingham and Sparrow, 2000). In aquatic or wetland ecosystems, clonal plants are often fragmented by natural or human disturbance, such as flood scouring or plowing (Barrat-Segretain et al., 1998; Combroux and Bornette, 2004; Klimešová and De Bello, 2009). Clonal fragments (such as rhizomes or aerial stems) can be effectively spread by water flow to recolonize new habitats (Barrat-Segretain and Bornette, 2000; Combroux and Bornette, 2004). Therefore, study on bud sprouting and plant growth is an important content in population ecology.

Present studies have mainly focused on the effects of clonal fragments (bud-bearing organs) on plant recruitment and have suggested that large clonal fragments have advantages in sprouting and plant growth over small ones (Hamdoun, 1972; Harris and Davy, 1986; Cordazzo and Davy, 1999; Dong et al., 2011; Weber, 2011; Lin et al., 2012). Clonal fragments in different soil layers may have the same capacity to initiate a new plant if the deep clonal fragments are taken up to soil surface by disturbance, such as plowing or grazing (Raju et al., 1964; Lodge, 2004). Buds usually form sequentially in size and age as well as nutrient and hormonal content along clonal fragments (McIntyre, 1970, 1972; Hendrickson and Briske, 1997). Theoretically, every bud can potentially initiate a new shoot to sustain population (Klimešová and Klimeš, 2007). However, the sprouting ability of buds may differ significantly due to different bud size (Vesk and Westoby, 2004). Larger buds represent a relatively large upfront investment in construction and maintenance, with relatively low activation costs and rapid resprouting response upon activation (Vesk and Westoby, 2004). The buds in shallow soil layer would be more active to sprout than those in deep soil layer (Klimeš et al., 1993). Therefore, the plant recruitment may be directly determined by the bud properties, such as bud size, vertical distribution in soil (Anderson et al., 2001; Lodge, 2004; Horvath, 2010). However, compared to clonal fragments, the

* Corresponding author at: Key Laboratory of Agro-ecological Processes in Subtropical Region, Institute of Subtropical Agriculture, The Chinese Academy of Sciences, Hunan 410125, China. Tel.: +86 731 84615203; fax: +86 731 84612685.
E-mail address: yonghongxie@163.com (Y. Xie).

0304-3770/$ – see front matter.
http://dx.doi.org/10.1016/j.aquabot.2012.08.004

effects of bud properties on plant regeneration have largely been overlooked (Vesk and Westoby, 2004).

The non-structural carbohydrate content (including starch and soluble sugar) in clonal fragments has been suggested as direct energy source to facilitate bud sprouting and plant growth (Suzuki and Hutchings, 1997; Suzuki and Stuefer, 1999; Klimešová and Klimeš, 2003; Palacio et al., 2007). However, buds may differ in energy storage and sprouting ability even if they locate on a same fragment due to different energy investment and origination (Vesk and Westoby, 2004). Large buds may contain more energy and sprout earlier due to earlier formation on rhizomes or stems (McIntyre, 1970; Zasada et al., 1994). However, the relationship between bud sprouting ability and non-structural carbohydrate content in buds is far from clear.

Miscanthus sacchariflorus (Maxim.) Hack., a typical rhizomatous clonal plant, is widely distributed in flooded wetlands in temperate regions in Asia, and has been known as an energy crop for its rapid growth (Atkinson, 2009). The rhizomes are usually fragmented through conventional soil cultivation to increase crop yield (Atkinson, 2009). The belowground axillary buds on rhizomes are main reproductive source of population recruitment (Nishihiro et al., 2004). After flooding, ramets regenerated from rhizome fragments were also observed away from the stands of *M. sacchariflorus* in Dongting Lake wetlands. After severe disturbance such as trenching in the wetlands, buds on rhizome fragments that have been taken to the surface soil layer can also sprout into shoots (personal observation). In the present study, we examined the effect of bud size (large and small) and vertical distribution in the soil layer (0–10 cm and 10–20 cm) on regenerative ability of *M. sacchariflorus* through a greenhouse sprouting experiment. Specifically, we test the following hypotheses: 1) sprouting ratio (*i.e.* the ratio of sprouted buds to total buds), plant height, accumulated biomass, starch and soluble sugar contents are higher in large than in small buds; 2) for buds of the same size, sprouting ratio, plant height, accumulated biomass, starch and soluble sugar contents are not different between the surface and deep soil layers.

2. Materials and methods

2.1. Study species

M. sacchariflorus (Poaceae), a perennial, rhizomatous C_4 grass, is widely distributed in temperate regions in Asia (Atkinson, 2009). *M. sacchariflorus* prefers wet habitats, such as flooded wetlands, roadside ditches, streams or ponds. This species usually forms tall monospecific stands, sprouting in March, growing rapidly from May to September, flowering from October to November and overwintering from December to February by belowground rhizomes. Vegetative growth is the primary reproductive strategy through buds formed in horizontal rhizomes in the 0–20 cm soil layer.

2.2. Experimental materials

The rhizomes were collected from a monodominant stand in Beizhouzi, in the east Dongting Lake (N 29°09′, E 112°46′) during 11–15 January, 2010, because the axillary buds developed on rhizomes had reached to a relatively stable size and were ready to sprout. Rhizomes in different soil layers (0–10 cm and 10–20 cm) in a 4 M × 4 M quadrat were excavated and stored in plastic bags, and immediately transported to laboratory (Kleyer et al., 2008). Rhizomes were carefully cleaned up by tap water to protect the integrity of axillary buds and rhizomes. After the axillary buds in different soil layers had been counted, rhizomes were cut into 3–4 cm long segments (an undamaged bud situated centrally) with similar fresh weight (9.78 ± 0.67 g per segment, mean ± S.E.) and diameter (1.14 ± 0.04 cm, mean ± S.E.). Bud size was measured by a vernier caliper. The buds in each soil layer were divided into two groups (small, <0.80 cm; large, >0.80 cm) according to the mean length of bud (0.80 cm). As a result, four types of buds (large or small buds in the 0–10 cm soil layer, large or small buds in the 10–20 cm soil layer) were used in the experiment.

2.3. Experimental design

Buds were planted in six plastic bins (50 cm in length, 40 cm in width and 30 cm in height) in a greenhouse, where the temperature was controlled at 25 ± 2 °C in the day and 17 ± 2 °C at night and the 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) in a 14 h photoperiod. Each bin was filled with 10 cm sediment, a mixture of sand and loam (1:1, v/v, containing 16% organic matter, 9.9 μg g^{-1} exchangeable N, 0.65 μg g^{-1} exchangeable P). Randomized block design with six replicates was applied. Each bin was divided into four blocks (50 cm in length, 10 cm in width and 30 cm in height for each block), and four types of buds were randomly and evenly planted into four blocks (10 buds per bud type and one bud type per block). The buds were then covered by 5 mm of the sediment. Bins were watered every day using tap water (pH 7.21, containing 4.3 μM NH_4^+–N, 16.8 μM NO_3^-N, 1.9 μM PO_4^{3-}P) to keep the substrate in moisture.

2.4. Sprouting and plant growth

Shoot emergence was recorded every day. The bud was considered as sprouting when a new shoot was higher than 0.5 cm. The experiment was ended after 55 days because no new shoot was sprouted after 45 days. At harvest, the heights of the three earliest emerging plants in each block were measured, and accumulated biomass of these plants were measured after drying at 65 °C for 48 h in an oven.

2.5. Measurement of non-structural carbohydrate content

Prior to experiment, the contents of soluble sugar and starch in each type of buds were measured. Ten buds from each bud type were chosen for measuring soluble sugar and starch contents, because it is difficult to measure the non-structural carbohydrate content in each bud, especially in small ones. Soluble sugar content was determined using a total hydrolysable reducing sugars method (Yemm and Willis, 1954). Bud samples were dried at 65 °C for 48 h in an oven and ground into 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.

2.6. Statistical analysis

All statistical analyses were performed using the software SPSS V18.0 (SPSS Inc., USA). The sprouting ratio of different bud size in each layer was analyzed by Binary Logistic Regression using bud size and soil layer as independent variables, since the bud sprouting success (*i.e.* whether the bud sprouts or not) is a binary variable (Bímová et al., 2003). Because plant height and biomass would reach a plateau at harvest time, the plant height and accumulated biomass at the harvest were analyzed by logarithmic regression, with bud size as independent variable and the effects of different bud size in two soil layers were analyzed by ANCOVA, with the bud size as a covariate (Rogosa, 1980). Non-structural forms

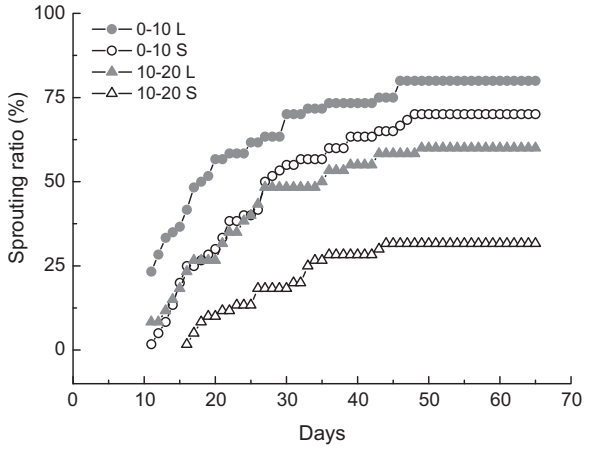

Fig. 1. Sprouting ratio from different bud sizes and different soil layers. 0–10 *L*, large buds from the 0 to 10 cm soil layer; 0–10 *S*, small buds from the 0 to 10 cm soil layer; 10–20 *L*, large buds from the 10 to 20 cm soil layer; 10–20 *S*, small buds from the 10 to 20 cm soil layer.

of carbohydrate in different bud types were analyzed by two-way ANOVAs, with bud size and soil layer as main factors. The relationships between non-structural carbohydrate and sprouting ratio or plant growth (plant height and accumulated biomass) were analyzed by Pearson correlation analysis (two-tailed test). The data were $\log_{10}$-transformed if necessary to reduce the heterogeneity of variances, and homogeneity was tested by Levene's test. Multiple comparisons of means (data at the end of the experiment) were performed by Tukey test at the 0.05 significance level.

3. Results

3.1. Sprouting ratio

Small buds from the 10 to 20 cm soil layer sprouted later than did the other three types of buds (17 *versus* 10 days, Fig. 1). Both bud size and soil layer had significant effect on final bud sprouting ratio ($P < 0.01$, Table 1). Sprouting ratio was highest in large buds from the 0 to 10 cm soil layer (80%), intermediate in small buds from the 0 to 10 cm layer (70%) and large buds from the 10 to 20 cm layer (60%), and lowest in small buds from the 10 to 20 cm layer (33.7%, Fig. 1A). The sprouting ratio was fitted well by logistic regression ($R^2 = 0.416$). Within each soil layer, sprouting ratio was higher in large than in small buds ($P < 0.01$, Table 1, Fig. 1A). For the buds of same size, the ratio was higher in the 0–10 cm than in the 10–20 cm soil layers ($P < 0.001$, Table 1, Fig. 1A). These data indicated that large buds and buds from the surface soil had a shorter sprouting time-lag and a higher sprouting ratio.

3.2. Plant height and accumulated biomass

Plant height and accumulated biomass were affected by bud size, with a significant interaction between bud size and soil layer ($P < 0.01$, Table 2), indicating that the effects of soil layer on plant growth depended on bud size. A logarithmic relationship existed between bud size and plant height or accumulated biomass in both soil layers (Fig. 2A and B). Plant height and accumulated biomass from large buds were higher than those from small ones ($P < 0.001$, Table 2, Fig. 2A and B). For large buds, plant height and accumulated biomass was not different between the two soil layers. For small buds, plant height and accumulated biomass was higher in the surface than in the deep soil layer ($P < 0.05$, Fig. 2A and B). These

Table 2
Factors affecting plant height and accumulated biomass with respect to bud size and soil layers. Main effects and their interaction were tested by ANCOVA.

Dependent variables	Bud size (*S*)	Layer (*L*)	*S* × *L*
Plant height (cm)	55.78**	0.03ns	16.79**
Accumulated biomass (g)	60.27**	0.17ns	20.33**
d.f.	1	1	1

** $P < 0.01$.
ns $P > 0.05$.

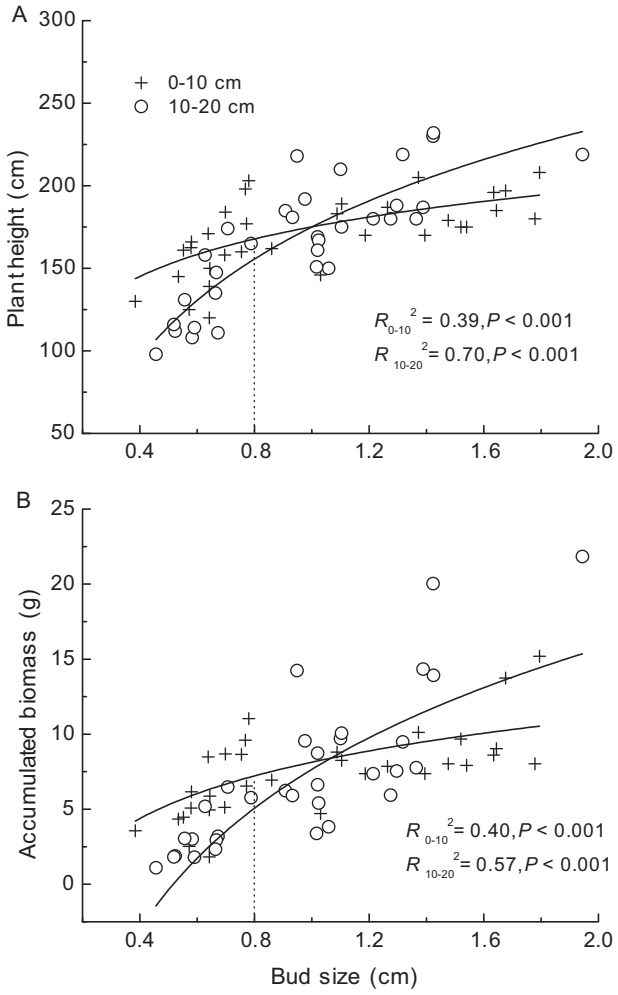

Fig. 2. Logarithmic regression of final plant height (A) and accumulated biomass (B) from different bud sizes in different soil layers.

Table 1
Factors affecting bud sprouting probability with respect to bud size and soil layers. Main effects and their interaction were tested by the binary logistic regression. $N = 240$.

Independent variables	*B*	Wald	*d.f.*	*P*	*Nagelkerke* R^2
Bud size (*S*)	2.66	8.88	1	0.003	0.416
Soil layer (*L*)	−3.86	12.12	1	<0.001	
S × *L*	3.14	4.97	1	0.026	
Constant	−1.02	2.35	1	0.361	

Table 3
Two-way ANOVA (*F*-values) of bud size and soil layer on initial non-structural carbohydrates and final plant height and accumulated biomass. Accumulated biomass was $\log_{10}$-transformed to meet the homogeneity of variances.

Dependent variables	Bud size (*S*)	Layer (*L*)	*S* × *L*
Soluble sugar content ($\mu g\,g^{-1}$)	13.93^{**}	41.93^{**}	2.62^{ns}
Starch content ($\mu g\,g^{-1}$)	1.19^{ns}	2.24^{ns}	0.56^{ns}
d.f.	1	1	1

** $P < 0.01$.
^{ns} $P > 0.05$.

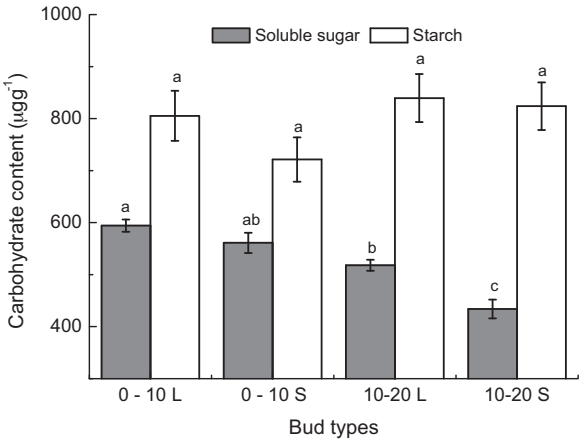

Fig. 3. The carbohydrate (soluble sugar and starch) contents (means ± S.E., $n = 3$) in different types of buds. 0–10 *L*, large buds from the 0 to 10 cm soil layer; 0–10 *S*, small buds from the 0 to 10 cm soil layer; 10–20 *L*, large buds from the 10 to 20 cm soil layer; 10–20 *S*, small buds from the 10 to 20 cm soil layer. Different letters indicate differences at the 0.05 significance level.

Table 4
Pearson correlation analysis between non-structural carbohydrate content and sprouting ratio or growth ($N = 12$). *r* represents the Pearson correlation coefficient. $N = 12$.

	Sprouting ratio (%)	Plant height (cm)	Accumulated biomass (g)
Soluble sugar content ($\mu g\,g^{-1}$)	0.937^{**}	0.773^{**}	0.781^{**}
Starch content ($\mu g\,g^{-1}$)	-0.237^{ns}	-0.503^{ns}	-0.485^{ns}

$^{**}P < 0.01$; $^{ns}P > 0.05$ (two-tailed).

results suggested that bud size was more important than depth in the soil in regulating plant growth.

3.3. Non-structural carbohydrate content

Soluble sugar content was higher in the buds from 0 to 10 cm (561.05–594.26 $\mu g\,g^{-1}$) than from 10 to 20 soil layers (433.90–517.97 $\mu g\,g^{-1}$, $P < 0.001$, Table 3, Fig. 3). At the same soil layer, soluble sugar content was higher in large buds than in small ones ($P < 0.01$, Table 3, Fig. 3). However, neither soil layer nor bud size had significant effects on starch content ($P > 0.05$, Table 3, Fig. 3).

3.4. Relationships between non-structural carbohydrate content and sprouting ratio or growth

Soluble sugar contents of buds were positively correlated with sprouting ratio ($r = 0.937$, $P < 0.001$), plant height ($r = 0.773$, $P = 0.003$) and accumulated biomass ($r = 0.781$, $P = 0.003$, Table 4). However, the correlation between starch contents of buds and sprouting ratio or plant height or accumulated biomass was insignificant ($P > 0.05$, Table 4).

4. Discussion

Sprouting ratio, plant height and accumulated biomass were higher in the large buds than in the small ones, which is consistent with our Hypothesis 1. These results might be related to the higher soluble sugar in large buds, as it supported by positive correlations between soluble sugar content and sprouting ratio, plant height or accumulated biomass. This result is consistent with that found in clonal fragments, which showed that large clonal fragments also had advantages in sprouting and plant growth (Dong et al., 2011; Weber, 2011). This may be ascribed to large clonal fragments can produce large buds due to a large amount of stored energy (Suzuki and Stuefer, 1999). However, earlier studies had neglected the effects of bud size and vertical distribution in soil layers on sprouting and plant growth. Actually, buds are produced sequentially along the rhizome, and bud size and age as well as nutrient and hormonal contents also have a gradient along the rhizome (McIntyre, 1970, 1972; Hendrickson and Briske, 1997; Klimeš et al., 1999). Younger and smaller buds, located on the distal portion of the rhizome, are more likely to grow out than do older and larger proximal basal buds due to the paradormancy (*i.e.* apical dominance or correlative inhibition) (Hendrickson and Briske, 1997; Horvath, 2010). However, the paradormancy would be released when the rhizomes were fragmented by natural or human disturbances, such as flooding scouring or plowing (Barrat-Segretain et al., 1998; Combroux and Bornette, 2004; Klimešová and De Bello, 2009; Horvath, 2010). Therefore, larger buds which contained higher soluble sugar content are more likely to sprout than do smaller buds, even though they are located on the same rhizome.

For large buds, plant height and accumulated biomass in the two soil layers were not significantly different. These results are partly consistent with our Hypothesis 2, which predicts that sprouting ratio, plant height, accumulated biomass, starch and soluble sugar contents are not different between the surface and deep soil layers for the buds with same size. Different to the plant fragments, deep soil layer buds had a lower sprouting ability than did surface layer buds. For buds from the deep soil layer, much energy should be depleted due to the high respiration rate under the anoxic condition (Klimeš et al., 1993; Hendrickson and Briske, 1997; Vesk and Westoby, 2004). Additionally, buds in the deep soil layer must face the risk of no sprouting forever when they are not taken back to the surface soil, which leads to a waste of energy. Therefore, the energy investment in deep layer buds might be lower according to the cost-benefit hypothesis (Vesk and Westoby, 2004). In our experiment, large buds in the deeper soil layer had less sugar content (517.97 $\mu g\,g^{-1}$) than did small ones in the surface layers (561.05 $\mu g\,g^{-1}$), which may result in a lower sprouting ratio than small buds in the surface layers (60% *versus* 70%, respectively). These results indicated that the lower soluble sugar content may lead to a lower sprouting ratio from buds in the deep soil layers (Vesk, 2006; Ott and Hartnett, 2011). However, the poor plant growth in small buds from deeper soil layer may be directly caused by the prolonged sprouting time-lag as suggested by Miller (1987).

Sprouting capacity, plant height and accumulated biomass were closely related to soluble sugar content, rather than starch content in buds, which is consistent with other studies. For example, sprouting capacity of *M. sacchariflorus* increased with increasing utilization of rhizome sugars (Suzuki and Stuefer, 1999). However, starch contents were not different among the four types of buds, suggesting that the bud sprouting ability of *M. sacchariflorus* might

not be influenced by starch content. This result is also consistent to a lignotuberous shrub *Erica australis*, showing that the starch reserves in lignotuber do not drive sprouting after clipping disturbance (Cruz et al., 2003). Starch usually cannot be utilized directly by the plant and must be transformed to soluble sugar for utilization (Karunagaran and Ramakrishna Rao, 1991; Hajirezaei et al., 2003). Therefore, starch content is usually decreased over several days after seed germination or bud sprouting (Smith et al., 2005; Zeeman et al., 2010). Therefore, initial soluble sugar content might be crucial for the initial plant growth due to the time lag by transforming starch into soluble sugar.

In this experiment, large buds sprouted earlier and had a higher plant growth rate, indicating that large buds (especially in the soil surface) might play a dominant role in expanding populations and competing for space in the favorable environments. Bud sprouting is limited by many environmental factors, and some of which might be catastrophic to populations (Cruz et al., 2003). Although small buds have a lower sprouting capacity and plant growth rate, they also take a supplement role in population recruitment after disturbance, which is an important strategy for the survival of population (Hamdoun, 1972; Bosela and Ewers, 1997; Klimešová and Martínková, 2004). Our field investigation have shown that 95% of rhizome buds of *M. sacchariflorus* was distributed in the 0–10 cm soil layer, and only 5% in the 10–20 cm soil layer (unpublished data), which might be an important strategy to deal with the trade-off between population expansion in favorable surface environments and survival of danger under occasionally unfavorable surface conditions.

Acknowledgements

The authors greatly appreciate E. Gross and two anonymous reviewers to provide constructive comments on a preliminary manuscript of this paper. This study was supported by the National Basic Research Program of China (2009CB421103, 2012CB417000) and the National Natural Science Foundation of China (31000143).

References

Anderson, J., Chao, W., Horvath, D., 2001. Review: A current review on the regulation of dormancy in vegetative buds. Weed Science 49, 581–589.
Atkinson, C., 2009. Establishing perennial grass energy crops in the UK: a review of current propagation options for *Miscanthus*. Biomass Bioenergy 33, 752–759.
Barrat-Segretain, M.H., Bornette, G., Hering-Vilas-Bôas, A., 1998. Comparative abilities of vegetative regeneration among aquatic plants growing in disturbed habitats. Aquatic Botany 60, 201–211.
Barrat-Segretain, M., Bornette, G., 2000. Regeneration and colonization abilities of aquatic plant fragments: effect of disturbance seasonality. Hydrobiologia 421, 31–39.
Bellingham, P.J., Sparrow, A.D., 2000. Resprouting as a life history strategy in woody plant communities. Oikos 89, 409–416.
Bímová, K., Mandák, B., Pyšek, P., 2003. Experimental study of vegetative regeneration in four invasive *Reynoutria* taxa (Polygonaceae). Plant Ecology 166, 1–11.
Bosela, M.J., Ewers, F.W., 1997. The mode of origin of root buds and root sprouts in the clonal tree *Sassafras albidum* (Lauraceae). American Journal of Botany 84, 1466–1481.
Choczynska, J., Johnson, E.A., 2009. A soil heat and water transfer model to predict belowground grass rhizome bud death in a grass fire. Journal of Vegetation Science 20, 277–287.
Combroux, I., Bornette, G., 2004. Propagule banks and regenerative strategies of aquatic plants. Journal of Vegetation Science 15, 13–20.
Cordazzo, C.V., Davy, A.J., 1999. Vegetative regeneration of *Panicum racemosum* from rhizome fragments on southern Brazilian coastal dunes. Journal of Coastal Research 15, 520–525.
Cruz, A., Pérez, B., Moreno, J.M., 2003. Plant stored reserves do not drive resprouting of the lignotuberous shrub *Erica australis*. New Phytologist 157, 251–261.
Dong, B.C., Liu, R.H., Zhang, Q., Li, H.L., Zhang, M.X., Lei, G.C., Yu, F.H., 2011. Burial depth and stolon internode length independently affect survival of small clonal fragments. PloS ONE 6, 1–6.
Hajirezaei, M.R., Börnke, F., Peisker, M., Takahata, Y., Lerchl, J., Kirakosyan, A., Sonnewald, U., 2003. Decreased sucrose content triggers starch breakdown and respiration in stored potato tubers (*Solanum tuberosum*). Journal of Experimental Botany 54, 477–488.
Hamdoun, A., 1972. Regenerative capacity of root fragments of *Cirsium arvense* (L.) Scop. Weed Research 12, 128–136.
Harris, D., Davy, A., 1986. Regenerative potential of *Elymus farctus* from rhizome fragments and seed. Journal of Ecology 74, 1057–1067.
Hendrickson, J.R., Briske, D.D., 1997. Axillary bud banks of two semiarid perennial grasses: occurrence, longevity, and contribution to population persistence. Oecologia 110, 584–591.
Horvath, D., 2010. Bud dormancy and growth. In: Pua, E.C., Davey, M.R. (Eds.), Plant Developmental Biology – Biotechnological Perspectives, vol. 1. Springer-Verlag, Berlin Heidelberg, pp. 53–70.
Karunagaran, D., Ramakrishna Rao, P., 1991. Mode and control of starch mobilization during germination of seeds of horse gram. Plant Science 73, 155–159.
Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G.M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Gotzenberger, L., Hodgson, J.G., Jackel, A.K., Kuhn, I., Kunzmann, D., Ozinga, W.A., Romermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O., Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E., Peco, B., 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. Journal of Ecology 96, 1266–1274.
Klimeš, L., Klimešová, J., Osbornová, J., 1993. Regeneration capacity and carbohydrate reserves in a clonal plant *Rumex alpinus*: effect of burial. Vegetatio 109, 153–160.
Klimeš, L., Klimešová, J., Cízková, H., 1999. Carbohydrate storage in rhizomes of *Phragmites australis*: the effects of altitude and rhizome age. Aquatic Botany 64, 105–110.
Klimešová, J., De Bello, F., 2009. CLO-PLA: the database of clonal and bud bank traits of Central European flora. Journal of Vegetation Science 20, 511–516.
Klimešová, J., Klimeš, L., 2003. Resprouting of herbs in disturbed habitats: is it adequately described by Bellingham–Sparrow's model? Oikos 103, 225–229.
Klimešová, J., Martínková, J., 2004. Intermediate growth forms as a model for the study of plant clonality functioning: an example with root sprouters. Evolutionary Ecology 18, 669–681.
Klimešová, J., Klimeš, L., 2007. Bud banks and their role in vegetative regeneration – a literature review and proposal for simple classification and assessment. Perspectives in Plant Ecology 8, 115–129.
Lin, H.F., Alpert, P., Yu, F.H., 2012. Effects of fragment size and water depth on performance of stem fragments of the invasive, amphibious, clonal plant *Ipomoea aquatica*. Aquatic Botany 99, 34–40.
Lodge, G.M., 2004. Response of *phalaris* to differing water regimes or grazing treatments as measured by basal bud weight, water-soluble carbohydrates, and plant tillers. Australian Journal of Agricultural Research 55, 879–885.
McIntyre, G.I., 1970. Studies on bud development in rhizome of *Agropyron repens*. 1. Influence of temperature, light intensity, and bud position on pattern of development. Canadian Journal of Botany 48, 1903.
McIntyre, G.I., 1972. Developmental studies on *Euphorbia esula* – influence of nitrogen supply on correlative inhibition of root bud activity. Canadian Journal of Botany 50, 949.
Miller, T.E., 1987. Effects of emergence time on survival and growth in an early old-field plant community. Oecologia 72, 272–278.
Nishihiro, J., Araki, S., Fujiwara, N., Washitani, I., 2004. Germination characteristics of lakeshore plants under an artificially stabilized water regime. Aquatic Botany 79, 333–343.
Ott, J.P., Hartnett, D.C., 2011. Bud production and dynamics of flowering and vegetative tillers in *Andropogon gerardii* (Poaceae): the role of developmental constraints. American Journal of Botany 98, 1293–1298.
Palacio, S., Maestro, M., Montserrat-Martí, G., 2007. Relationship between shoot-rooting and root-sprouting abilities and the carbohydrate and nitrogen reserves of Mediterranean dwarf shrubs. Annals of Botany 100, 865–874.
Raju, M., Steeves, T., Coupland, R., 1964. On the regeneration of root fragments of leafy spurge (*Euphorbia esula* L.). Weed Research 4, 2–11.
Rogosa, D., 1980. Comparing nonparallel regression lines. Psychological Bulletin 88, 307–321.
Smith, A.M., Zeeman, S.C., Smith, S.M., 2005. Starch degradation. Annual Review of Plant Biology 56, 73–98.
Suzuki, J.L., Hutchings, M.J., 1997. Interactions between shoots in clonal plants and the effects of stored resources on the structure of shoot populations. In: de Kroon, H., van Groenendael, J. (Eds.), The Ecology and Evolution of Clonal Plants. Backhuys Publishers, Leiden, pp. 311–329.
Suzuki, J.I., Stuefer, J., 1999. On the ecological and evolutionary significance of storage in clonal plants. Plant Species Biology 14, 11–17.
Vesk, P.A., Westoby, M., 2004. Funding the bud bank: a review of the costs of buds. Oikos 106, 200–208.
Vesk, P.A., 2006. Plant size and resprouting ability: trading tolerance and avoidance of damage? Journal of Ecology 94, 1027–1034.

Weber, E., 2011. Strong regeneration ability from rhizome fragments in two invasive clonal plants (*Solidagocanadensis* and *S. gigantea*). Biological Invasions 13, 1–9.
Yemm, E., Willis, A., 1954. The estimation of carbohydrates in plant extracts by anthrone. Biochemical Journal 57, 508–514.
Zasada, J.C., Tappeiner Iii, J.C., Maxwell, B.D., Radwan, M., 1994. Seasonal changes in shoot and root production and in carbohydrate content of salmonberry (*Rubus spectabilis*) rhizome segments from the central Oregon Coast Ranges. Canadian Journal of Forest Research 24, 272–277.
Zeeman, S.C., Kossmann, J., Smith, A.M., 2010. Starch: its metabolism, evolution, and biotechnological modification in plants. Annual Review of Plant Biology 61, 209–234.