Effects of sediment burial disturbance on the vegetative propagation of Phalaris arundinacea with different shoot statuses

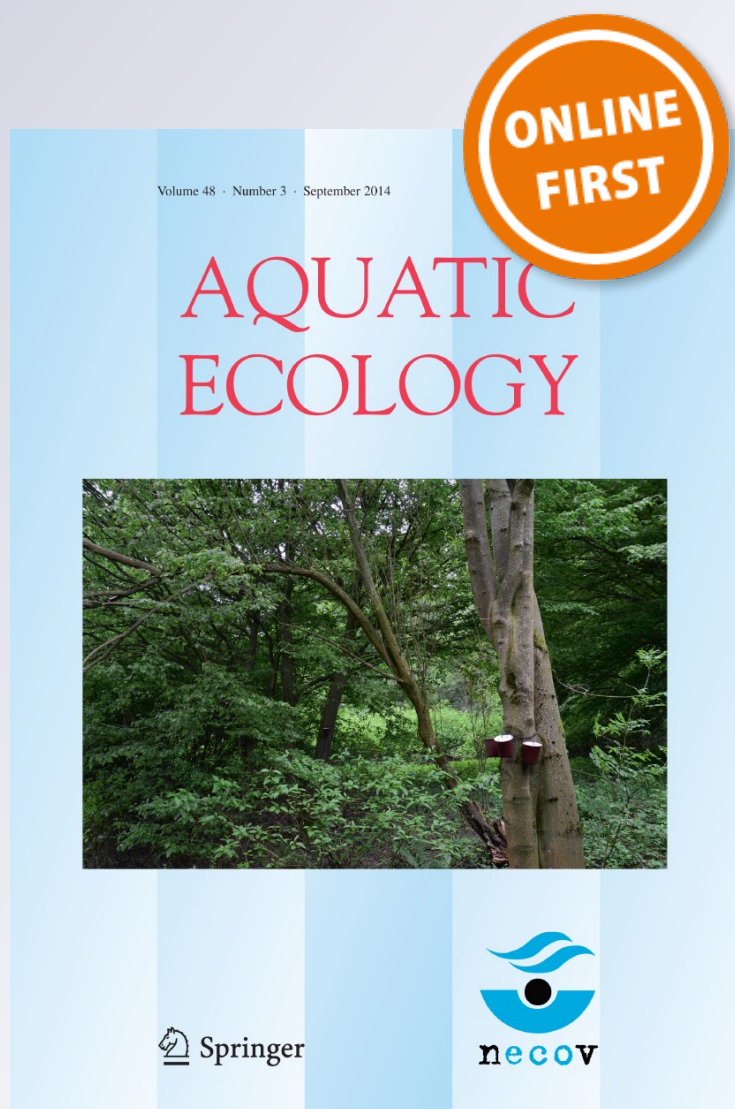## Xinsheng Chen, Zhengmiao Deng, Yonghong Xie, Feng Li, Zhiyong Hou, Xu Li & Y. F. Li

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Abstract Shoot status, such as orientation and connection to the root system, and sediment burial depth after flooding disturbances have important ecological consequences on the post-flooding growth and vegetative reproduction of emergent macrophytes in wetlands. In the present study, we investigated the effect of shoot status (vertical, prostrate, or detached) and sediment burial depth (0.5 or 10 cm) on biomass accumulation and propagule production in *Phalaris arundinacea* (Poaceae) using an outdoor mesocosm system. In contrast to our prediction that shallow sediment burial would activate the axillary buds on prostrate shoots and regenerate more ramets, significantly fewer new ramets, rhizomes, buds, and biomass accumulation formed in *P. arundinacea* as the shoots changed from vertical to prostrate. Deeper sediment burial resulted in lower biomass and propagule production in plants with prostrate shoots, whereas vertical shoots increased the number of ramets. *P arundinacea* with detached shoots also produced a number of propagules after shallow or deep sediment burial, which might be important for the long-distance dispersal of *P. arundinacea*. These results suggest that *P. arundinacea* is a potentially invasive species in many lacustrine wetlands, particularly those with a high sedimentation rate, due to its high capacity for vegetative propagation.

Keywords Shoot orientation · Clonal plants · Reed canarygrass · Vegetative reproduction · Sediment burial

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Introduction

Sedimentation is a common phenomenon in wetlands because of changes in the water level, sediment input, and the settlement of suspended particles (Maun 1998). The depth of sedimentation in wetlands ranges from a few mm to several cm per year, depending on management practices such as forest conservation or

the agricultural cultivation of watersheds (Maun 1998). A previous study in lacustrine wetlands demonstrated that sediments were often transported by flow waters from connecting rivers during flooding periods (Li and Xie 2009). Additional reports demonstrated that, after flooding, propagules, seedlings, plant fragments, and adult plants were buried within the sediment to varying extents depending on the magnitude of the disturbance (Combroux et al. 2001; Mou and Sun 2011).

Sediment burial is a major selective force, and wetland plants have evolved a variety of adaptations that allow their survival, growth, and reproduction during normal sediment accretion (Maun 1998; Mou and Sun 2011). In response to burial, clonal macrophytes, which are a common feature of wetland habitats, might elongate their shoot internodes, petioles, leaf sheaths, leaves, spacers, and rhizomes, increase the number of shoot nodes, and activate dormant buds on their shoots (Maun 1996, 1998; Li and Xie 2009; Chen et al. 2011). This allows growth out of the sediment surface and escape from sedimentation stress.

Among the different vegetative parts of macrophytes, shoots are probably the most vulnerable, because they are easily damaged, broken, or flattened by flooding disturbances (Madsen et al. 1988; Riis et al. 2009). After flooding disturbances, the orientation of shoots ranges from horizontal to vertical, and their connection to belowground parts varies from intact to detached. These shoot statuses might have different ecological consequences on post-flooding growth and vegetative reproduction (Decruyenaere and Holt 2001; Dong et al. 2010), but has rarely been tested by empirical studies. Shoots that remain attached to the belowground parts but lay prostrate in shallow moist soil might have the opportunity to regenerate new ramets from axillary buds (Decruyenaere and Holt 2001; Wijte et al. 2005; Thomas and Hay 2010). Therefore, flooding induced prostrate growth might increase the number of ramets that are produced by caulescent macrophytes after shallow sedimentation. Once detached, shoots cannot receive resources such as water and nutrients from the belowground parts; therefore, they can only use stored reserves for regeneration (Song et al. 2013). As such, the chance of establishment from detached shoots would be reduced. Upon deep sediment burial, horizontal

shoots suffer more physical stress than vertical shoots, and regeneration from horizontal shoots requires more stored resources (Nzunda et al. 2008). Therefore, plants with horizontal shoots would produce fewer ramets than those with vertical shoots after deep sedimentation.

Phalaris arundinacea (Poaceae) is distributed widely in marshes, rivers, and lake margins in temperate parts of the northern hemisphere, which are often disturbed by sedimentation (Kercher and Zedler 2004; Wu and Phillips 2006). In addition to seed and rhizome reproduction, *P. arundinacea* can produce roots and upright branches from its main shoots that have been flattened by disturbances (Zedler and Kercher 2004; Herr-Turoff and Zedler 2007). In the present study, we investigated the effect of shoot status (vertical, prostrate, or detached) and sediment burial depth (0.5 or 10 cm) on the growth and vegetative reproduction of *P. arundinacea*. Specifically, we tested the following hypotheses: (1) After shallow sedimentation, the number of propagules produced by *P. arundinacea* is increased when shoots change from vertical to horizontal, but decreased when shoots are disconnected with their belowground parts; (2) upon deep sediment burial, the number of propagules produced by plants with prostrate or detached shoots is lower than those with vertical shoots. To test these hypotheses, two levels of sediment burial (0.5 and 10 cm) and three shoot statuses (vertical, prostrate, and detached) were applied to *P. arundinacea* to investigate the changes in growth and vegetative reproduction.

Materials and methods

The study species

Culms of *Phalaris arundinacea* (Poaceae) are reed-like, leafy, and 0.6–1.5 m in height (Wu and Phillips 2006). Their rhizomes spread extensively. *P. arundinacea* flowers and fruits from April to June in the Dongting Lake wetlands, but seedlings are rare (Hou et al. 2012). In addition to seed and rhizome reproduction, *P. arundinacea* forms roots in the axils of its branches. Both branches and node-bearing plant fragments can establish new plants (Zedler and Kercher 2004).

Experimental design

Plants were excavated from ~5 m^2 of East Dongting Lake wetlands, Liumenzha, on February 22, 2013. One hundred young ramets (3–4 leaves, ca.15 cm) with intact root systems were transported to the Dongting Lake Station for Wetland Ecosystem Research, the Chinese Academy of Sciences, Yueyang, Hunan Province, China. Each ramet was planted in a plastic container (18 cm in height and 25 cm in diameter) that was filled with 10 cm soil. On March 21, 48 similar sized plants (7–9 leaves, 47–57 cm in height without branches) were selected for the experiment. A randomized block design using eight replicates was applied. Eight outdoor water tanks (100 cm × 90 cm × 60 cm) filled with 10 cm soil were used. Each tank was divided into six blocks (each block was sized 100 cm in length, 15 cm in width, and 60 cm in height), and six ramets were randomly planted into the six blocks (one plant per block). Tap water was added to each tank to achieve a 60-cm water level to simulate flooding disturbance. One week later, the water in the tank was removed. Two levels of sediment burial (0.5 and 10 cm) and three shoot statuses (vertical, prostrate, and detached) were then randomly applied to the six plants in each tank. Prostrate shoots were obtained by laying the shoot horizontally along the soil surface, and detached shoots were obtained by cutting the shoot at the soil surface and then placing it horizontally.

All soil used in the experiment was exhumed from the upper layer of the *P. arundinacea* community where the ramets were excavated. The soil consisted of 1.35 % organic matter, 0.09 % total nitrogen, and 0.05 % total phosphorus. The water level in the tanks was maintained at 10 cm (0 cm for the plant). Tap water was added as needed, and surplus water was removed after rain to control the water level. Plants were checked each week, and new ramets were marked with plastic tags. Meteorological data were recorded by automatic weather station (Milos 520, Vaisala, Finland) located ca. 150 m away from the experiment. During the experiment (March 21–May 23, 2013), daily air temperature was 19.0 ± 4.4 °C (mean ± SD), and photosynthetically active radiation (PAR) was 21.7 ± 11.4 mol m^{-2} s^{-1} (mean ± SD).

Harvest and measurement

The plants were harvested on May 23, 8 weeks after treatment. The plants were carefully excavated from the tanks to maintain the connection between ramets. The plants were then cleaned with tap water and transported to the laboratory for measurements. The number of ramets, rhizomes, rhizome buds, and shoot nodes, and the length of new ramets produced by each plant were recorded. Each plant was then separated into shoots, roots, and rhizomes. The biomass of each plant part was measured after drying at 80 °C for 48 h in an oven. Plants with any live aboveground material were defined as alive. Biomass accumulation was calculated as the total plant dry weight at the end of the experiment. Biomass allocation was calculated as the mass of each plant organ, i.e., shoot, root, and rhizome, relative to the biomass of the total plant.

Data analysis

The effect of burial depth and shoot status on biomass accumulation, biomass allocation, length of new ramets, and the number of new ramets, rhizomes, buds, and shoot nodes was assessed using a general linear model (GLM). Multiple comparisons of means were performed using Tukey's test at the 0.05 significance level, and a Bonferroni correction for multiple comparisons was made where appropriate. Data were log^{10}-transformed if necessary to reduce the heterogeneity of variances, and homogeneity was tested using Levene's test. All statistical analyses were performed using the SPSS 15.0 package (SPSS Inc., USA).

Results

Biomass accumulation and allocation

Regardless of sediment depth, 100 % of the plants with vertical or prostrate shoots survived, and 75 % of those with detached shoots survived. For dead plants, the shoots were partially rotten and no ramets were regenerated from belowground parts. Both shoot status and burial depth significantly affected *P. arundinacea* biomass accumulation, shoot biomass, root biomass, and rhizome biomass, with significant

Table 1 Summary of two-way ANOVA (F values) for biomass accumulation, biomass allocation, the length of ramets, and the number of ramets, rhizomes, rhizome buds, and shoot nodes in *Phalaris arundinacea* growing at two sedimentation depths with three shoot statuses

Effect	Biomass accumulation	Shoot mass	Root mass	Rhizome mass	Shoot mass ratio	Root mass ratio	Length of ramets	No. of ramets	No. of rhizomes	No. of buds	No. of shoot nodes
Shoot status (S)	219.63***	187.88***	105.29***	229.27***	0.12ns	0.76ns	3.83*	112.70***	29.82***	90.61***	80.32***
Burial depth (B)	27.58***	27.72***	11.31**	11.23**	5.61*	4.52*	2.21ns	9.80**	20.87***	2.64ns	14.52***
S × B	12.05***	10.37***	7.17**	11.55***	0.77ns	0.91ns	0.50ns	12.92***	4.72*	6.34**	6.92**

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; ns $P > 0.05$

interactions between burial depth and shoot status (Table 1; Fig. 1a–d). At the same burial depth, the biomass accumulation was highest in plants with vertical shoots, intermediate in plants with prostrate shoots, and lowest in plants with detached shoots (Fig. 1a). Interestingly, the effect of burial depth was dependent on shoot status. Deeper burial reduced the biomass of plants with prostrate or detached shoots, but had no effect on those with vertical shoots. Statistically, *P. arundinacea* biomass allocation was only affected by burial depth ($P < 0.05$; Table 1). Changes in shoot mass, root mass, and rhizome mass had a similar trend as biomass accumulation (Fig. 1b–d). The shoot mass ratio was higher in plants with prostrate shoots and 0.5 cm burial compared with those with detached shoots and 10 cm burial.

The number of new ramets, rhizomes, buds, and shoot nodes

Both shoot status and burial depth affected the number of new ramets, rhizomes, and shoot nodes produced by *P. arundinacea*, with significant interactions between burial depth and shoot status (Table 1; Fig. 2a, c, e). At the same burial depth, the number of new ramets was highest in plants with vertical shoots, intermediate in plants with prostrate shoots, and lowest in plants with detached shoots (Fig. 2a). The effect of burial depth was dependent on shoot status. Deeper burial significantly increased the number of new ramets in plants with vertical shoots, but reduced the number in plants with prostrate or detached shoots. Statistically, the length of new ramets was only affected by shoot status (Table 1; Fig. 2b). At the 0.5 cm burial depth, new ramets were longer in plants with vertical shoots compared to those with detached shoots. At 10 cm burial depth, the length of new ramets was not significantly different among the three shoot statues (Fig. 2b).

At the same burial depth, the number of rhizomes produced by plants with vertical shoots was higher than those produced by plants with prostrate or detached shoots (Fig. 2c). Deeper burial led to a decreased number of rhizomes in plants with prostrate or detached shoots, but not in those with vertical shoots.

At the same burial depth, the number of shoot nodes was highest in plants with vertical shoots, intermediate in plants with prostrate shoots, and lowest in plants
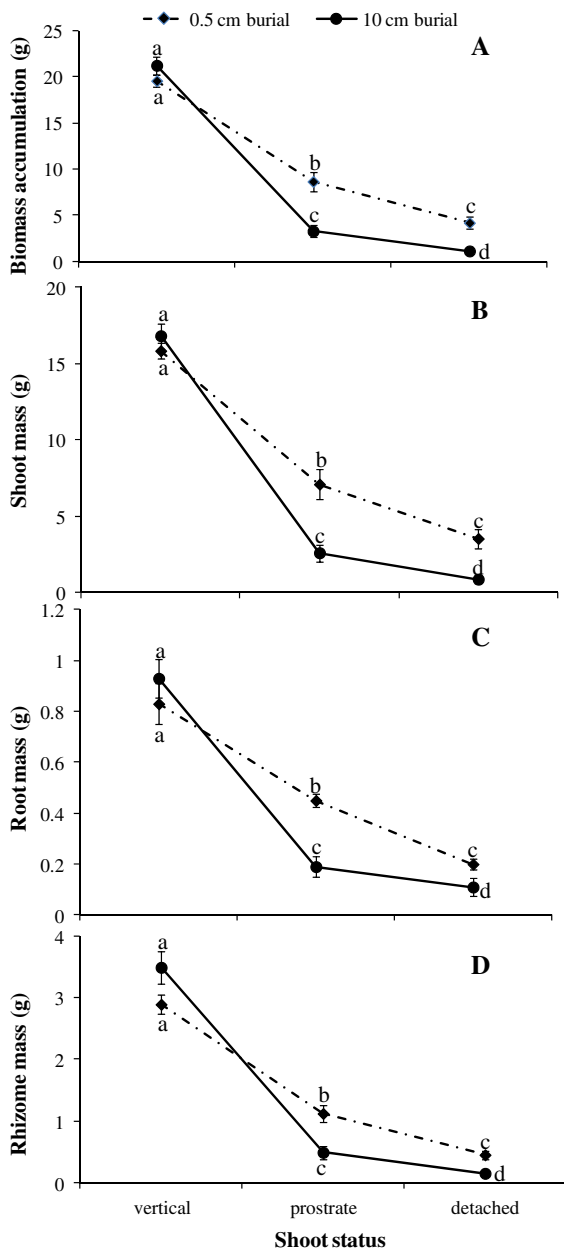
Fig. 1 The effect of burial depth on biomass accumulation, shoot biomass, root biomass, and rhizome biomass in *Phalaris arundinacea* with different shoot statuses. *Standard error bars* sharing the same *lower case letters* are not significantly different (*P* > 0.05)

with detached shoots (Fig. 2e). Deeper burial reduced the number of shoot nodes in plants with prostrate or detached shoots, but not in plants with vertical shoots.
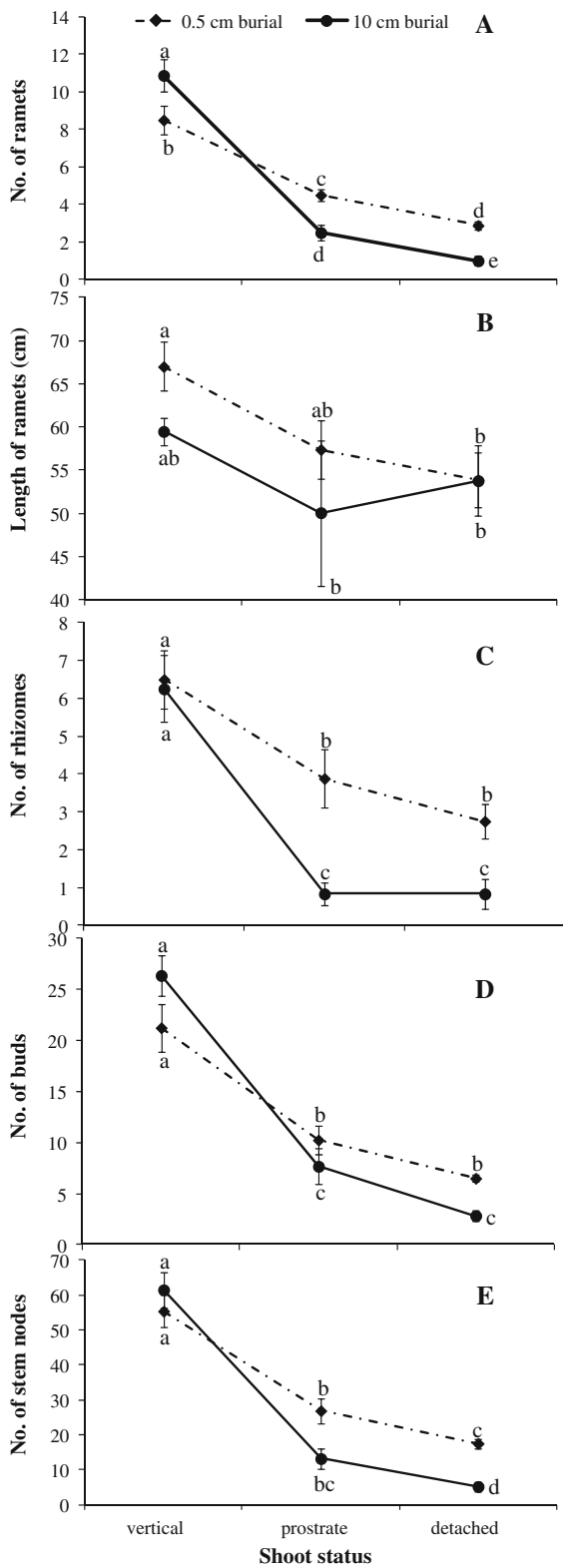
The number of buds produced by *P. arundinacea* was affected by shoot status, with significant

interactions between shoot status and burial depth (Table 1; Fig. 2d). The number of buds produced by plants with vertical shoots was higher than by those produced by plants with prostrate or detached shoots. Deeper burial reduced the number of buds only in plants with detached shoots.

Discussion

After shallow sediment burial, the biomass and propagule production in *P. arundinacea* were significantly reduced as shoots changed from vertical to prostrate. This invalidated our original hypothesis, which predicted that axillary buds on prostrate shoots would activate and sprout into ramets upon exposure to shallow moist sediment. Below- and/or aboveground resources, particularly non-structural carbohydrates, are essential for re-sprouting after disturbance (Decruyenaere and Holt 2001; Nzunda et al. 2008; Clarke et al. 2013; Deng et al. 2013). Prostrate growth might disrupt the normal distribution of leaves and break roots on the side opposing the prostrate shoot (Nzunda et al. 2008). Consequently, photosynthesis and the manufacture of carbohydrates in plants with prostrate shoots were suppressed (Perumal and Maun 2006). Although the buds on the prostrate shoots that contact with the moist soil have the potential to sprout, this capacity might be constrained by the lack of carbohydrates. In addition, if the pathway of substance exchange between the aboveground and belowground parts was cut, the likelihood of establishment from the detached shoots and rhizomes would be further reduced, as shown previously in the perennial grass *Arundo donax* (Decruyenaere and Holt 2001).

Deeper burial incurred a lower biomass and propagule production in plants with prostrate or detached shoots, but not vertical shoots. These results support our second hypothesis, which predicted that deeper burial would have more negative effects on plants with prostrate or detached shoots. High sedimentation results in only partial burial of plants with vertical shoots; therefore, they can maintain a photosynthetic leaf area aboveground (Maun 1998; Gilbert et al. 2011). However, plants with prostrate shoots incur complete burial. The growing tips of the prostrate shoots need to regain a vertical orientation to be able to re-sprout and emerge from the sediment surface first

◄**Fig. 2** The effect of burial depth on the number of ramets, rhizomes, rhizome buds, and shoot nodes produced by *Phalaris arundinacea* with different shoot statuses. *Standard error bars* sharing the same *lower case letters* are not significantly different ($P > 0.05$)

(Nzunda et al. 2008). During this emergence, the energy required for re-sprouting relies totally on the resources stored in the shoots and/or rhizomes to allow respiration and re-growth until the plant recovers the photosynthetic capacity to support these processes (Chapin et al. 1990; Maun 1998). Beyond the burial threshold, plants might fail to emerge because the carbohydrate reserves in storage organs are completely depleted (Klimeš et al. 1993).

In contrast to *P. arundinacea* with horizontal shoots, those with vertical shoots produced more ramets when buried by 10 cm, suggesting that partial burial stimulates propagule production of *P. arundinacea*. The stimulating effect of sediment burial on plant growth has been reported for several clonal macrophytes in coastal ecosystems (Maun 1998; Deng et al. 2008). Enhanced plant vigor following burial might be attributed to increased soil volume, soil resources, activity of mycorrhizal fungi, and a reactive growth response by the plant to burial (Maun 1998). The sedimentation rate has been increasing in many wetlands, particularly in developing countries, because of agricultural activity or the deterioration of vegetation drainage (Atapattu and Kodituwakku 2009; Cui et al. 2013). For example, sediment can accrete 3–7 cm annually during flooding times in the Dongting Lake wetlands where this study was performed (Li et al. 2008). *P. arundinacea* might benefit from the increased sedimentation rate by producing more ramets. Therefore, wetlands with enhanced sediments are particularly vulnerable to invasion by this species (Kercher and Zedler 2004).

The number of propagules produced by *P. arundinacea* with disconnected shoots and belowground parts (rhizomes and roots) was much lower than that produced by intact plants, regardless of burial depth. However, these propagules might have specific importance for the long-distance dispersal of *P. arundinacea* (Galatowitsch et al. 1999; Paveglio and Kilbride 2000; Zedler and Kercher 2004). The hollow shoots of *P. arundinacea* are fragile and easily broken by storms, winds, and mechanical stresses (Zedler and Kercher 2004). Therefore, detached shoots might be

carried away to other sites by floodwater. As long as the sites are suitable for colonization, *P. arundinacea* might establish and expand intensively through its newly developed rhizome system in new habitats to form monotypic stands (Kercher and Zedler 2004).

Phalaris arundinacea can produce propagules when shoots changed from vertical to prostrate, even when detached from parent plants. Furthermore, deeper sediment burial increased the number of ramets in plants with vertical shoots. These results suggest that *P. arundinacea* is a potentially invasive species in many lacustrine wetlands, particularly those with a high sedimentation rate, due to its high capacity for vegetative propagation.

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