

Belowground bud banks of four dominant macrophytes along a small-scale elevational gradient in Dongting Lake wetlands, China

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ABSTRACT

Belowground bud banks play a fundamental role in the population dynamics of clonal wetland macrophytes. We investigated the size and seasonal dynamics of the belowground bud banks of four dominant macrophytes along a small-scale elevational gradient in Dongting Lake wetlands, China. The belowground bud banks of all four species were found to peak in January, the coldest month of the year. Bud banks were densest for low-elevation *Phalaris arundinacea* L. (1049 ± 70 buds m^{-2}), intermediate for mid-elevation *Carex brevicuspis* C.B. Clarke and *Polygonum hydropiper* L. (565 ± 52 buds m^{-2} and 484 ± 78 buds m^{-2} , respectively), and lowest for high-elevation *Miscanthus sacchariflorus* (Maxim.) Hackel (333 ± 52 buds m^{-2}). Elevation, which reflects stand flooding regimes, explained 85% of the variability in bud bank size among the four species. The bud bank size of *C. brevicuspis*, *P. hydropiper*, and *P. arundinacea* decreased markedly after the spring sprout, thus indicating that these three species may be sensitive to the timing of disturbance. Bud bank densities for all four species were lowest just before flooding (in May), which might be a strategy to reduce maintenance costs through the flooding season (June–October). Among the four species examined, the bud bank density of *P. arundinacea* was highest during the growing season, which suggests that this species may be the most resilient to environmental change.

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1. Introduction

In perennial-dominated grasslands and many other herbaceous communities, the belowground population of meristems (the “bud bank” sensu Harper, 1977) plays a fundamental role in local plant population persistence, structure, and dynamics (Benson et al., 2004; Dalgleish and Hartnett, 2006; Zhang et al., 2009; Ott and Hartnett, 2012). Bud banks vary in size and composition among communities, and can closely reflect changes in aboveground plant abundance and species composition in grasslands (Benson et al., 2004; Dalgleish and Hartnett, 2009). Thus, understanding differences in bud banks among communities should be important for understanding regional as well as local patterns, such as gradients in productivity and changes in vegetation distribution (Dalgleish and Hartnett, 2006).

Wetland plants reproduce predominantly by vegetative reproduction and bud banks as a consequence of phylogeny, life history constraints, and/or adaptation to wet habitats (Sosnová et al., 2010). In natural wetlands, emergent macrophytes experience seasonal changes in abiotic environments, such as changes in water level and temperature. To acclimate to seasonal changes in wetland habitats, emergent macrophytes may adjust the demography of bud banks to regulate shoot population dynamics and productivity (Deng et al., 2013a; Chen et al., 2014a). For example, the bud density of *Carex brevicuspis* is lowest just before flooding in Dongting Lake wetlands, China (Chen et al., 2014a). However, the responses of bud banks to flooding differ among species, even for co-occurring emergent macrophytes (Lenssen et al., 2000; Chen et al., 2014b).

In freshwater wetlands, plant growth, vegetative reproduction, and distribution are closely related to hydrological gradients, which are closely associated with the elevation at which plants occur (Lenssen et al., 2000; Urban, 2005; Deng et al., 2013a). A small-scale elevational gradient was shown to impact the size and composition of bud banks within *C. brevicuspis* populations in Dongting Lake wetlands (Deng et al., 2013a). Inter-specifically, species distributed in low-elevation sites may experience long periods of submergence,

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which results in a small number of viable shoots (Macek et al., 2006). Thus, a large bud bank may be necessary for low-elevation species to ensure complete replacement of aboveground shoots after flood waters recede.

In temperate wetlands, low temperatures constrain the growth of aboveground shoots. Energy, such as carbohydrates, may be translocated from aboveground shoots to belowground storage organs (rhizomes, etc.) at the end of the growing season (Roseff and Bernard, 1979; Bernard, 1990). A large reserve of belowground bud banks in winter may enable macrophytes to live through the cold winter, and facilitate shoot population recruitment in spring. The phenology of belowground bud production is largely unknown for wetland macrophytes, and thus empirical studies are needed to test these hypotheses.

In the present study, we investigated the demography of the belowground bud banks of four dominant macrophytes in Dongting Lake wetlands. The wetlands are characterized by a long flooding season (June–October) and a cold winter (December–February). Within these wetlands, *Phalaris arundinacea* L. tends to dominate low elevations, *C. brevicuspis* C.B. Clarke and *Polygonum hydropiper* L. dominate intermediate areas, and *Miscanthus sacchariflorus* (Maxim.) Hackel dominates high elevations (Peng et al., 1984; Xie and Chen, 2008). Specifically, we tested two hypotheses. First, we hypothesized that the low-elevation *P. arundinacea* would have a larger bud bank than the high-elevation *M. sacchariflorus*, because a larger number of shoots need to be replaced in low-elevation sites after longer periods of submergence. Second, we hypothesized that the bud bank density should be relatively high in winter because a large number of buds are necessary for aboveground population recruitment in spring. In contrast, density should be relatively low after the spring sprout because a large number of buds would have sprouted into shoots. To test these hypotheses, we investigated bud bank demography over one complete growing season by sampling belowground bud and aboveground shoot populations of the aforementioned four species immediately after flooding (November), in winter (January), in spring (March), and before flooding (May).

2. Materials and methods

2.1. Study species

P. arundinacea (Poaceae), a perennial rhizomatous C_3 grass, is distributed widely in marshes, rivers, and lake margins in temperate regions of the northern hemisphere (Wu and Phillips, 2006). It is characterized by extensively creeping rhizomes, and has leafy, reed-like culms that are 0.6–1.5 m in height. *C. brevicuspis* (Cyperaceae) is a perennial rhizomatous sedge that is distributed in the wetlands of eastern mainland China and Taiwan (Dai et al., 2010). The pseudoculm of this plant, which is made up of a series of overlapping leaf sheaths, is typically 20–55 cm in height. *P. hydropiper* (Polygonaceae) is described as an annual herb, but it produces overwintering belowground rhizomes in the Dongting Lake wetlands (Li et al., 2003; Chen et al., 2014b). The branched stems of *P. hydropiper* are normally 40–70 cm in height. *P. hydropiper* typically occurs as a co-dominant with *Carex* species, and patches can be found

embedded in stands of *C. brevicuspis* (Chen et al., 2014b). *M. sacchariflorus* (Poaceae), a perennial, rhizomatous C_4 grass, is widely distributed in the temperate regions of Asia (Atkinson, 2009). The culms of this species are slender, erect, and 100–500 cm in height. The aforementioned four species often form monodominant communities along elevational gradients in the Dongting Lake wetlands. Although all four species can flower and fruit in the Dongting Lake wetlands, seedlings are rarely observed in the field (Chen et al., 2011; Hou et al., 2012).

2.2. Study sites

Dongting Lake (28°30′–30°20′N, 111°40′–113°10′E), the second largest freshwater lake in China, is located in the northern Hunan Province (Fig. 1). It lies in a basin to the south of the Yangtze River, and is connected to the Yangtze by distributary channels. The surrounding wetlands are characterized by large seasonal fluctuations in water levels (up to 15 m); they are completely flooded from June to October and exposed from November to the following May. The mean annual temperature is 16.8 °C, with hot summers (June–August, 27.3 °C) and cold winters (December–February, 5.8 °C) (Huang et al., 2013). Annual precipitation is 1382 mm, with more than 60% falling between April and August.

Three lake shores where the four study species exhibit clear elevational zonation—Beizhouzi (29°10′31.4″N, 112°47′55.9″E), Chapanzhou (28°54′11.8″N, 112°48′34.6″E), and Tuanzhou (29°20′20.8″N, 112°51′05.4″E)—were selected as study sites (Fig. 1). At each site, a 1-km transect parallel to the lake shore was established in the middle of each species zone. The elevation of each transect was acquired from a Digital Elevation Model (1:1 0000) of Dongting Lake in 1995 produced by Changjiang Water Resources Commission (Ministry of Water Resources, China) according to the geographical coordinates. Theoretically, if the water level exceeds a certain elevation, vegetation at this elevation can be considered as submerged (Xie et al., 2014). The submergence duration of each species (sampling transect) was calculated on the basis of daily water level at Chenglingji hydrological gauging station in 2010. The mean flooding depth of each species was calculated as the average of water level minus the elevation where the species (sampling transect) occurs during the flooding season. The elevation, submergence duration, and mean flooding depth of the four dominant macrophytes at our study sites are given in Table 1.

2.3. Aboveground and belowground sampling

Five random points along each transect were chosen for destructive shoot and belowground bud sampling. The minimum distance between sampling points was 100 m. For *P. hydropiper*, which does not form distinct species zone, five patches within the *C. brevicuspis* transect were chosen for sampling. The geographical information of each sampling point was recorded using a handheld GPS (UniStrong Odin Series, Beijing, China). On each sampling date, one randomly selected quadrat [25 cm × 25 cm for *P. arundinacea*, *P. hydropiper*, and *C. brevicuspis*, and 50 cm × 50 cm for *M. sacchariflorus* (due to relatively large individual size)] was

Table 1
Elevation, submergence duration, and mean flooding depth of four dominant macrophyte species at our study sites in the Dongting Lake wetlands, China.

Species	Elevation (m)	Submergence duration (day)	Mean flooding depth (m)
<i>Phalaris arundinacea</i>	23.62 ± 0.75 ^b	211.5 ± 9.5 ^a	4.92 ± 0.53 ^a
<i>Carex brevicuspis</i>	25.09 ± 0.23 ^{ab}	184.0 ± 8.2 ^{ab}	4.06 ± 0.05 ^{ab}
<i>Polygonum hydropiper</i>	25.44 ± 0.44 ^{ab}	177.0 ± 11.8 ^{ab}	3.88 ± 0.18 ^{ab}
<i>Miscanthus sacchariflorus</i>	28.10 ± 1.59 ^a	113.3 ± 37.7 ^b	2.60 ± 0.79 ^b

Different letters indicate differences at the 0.05 significance level ($n = 3$, Tukey test).

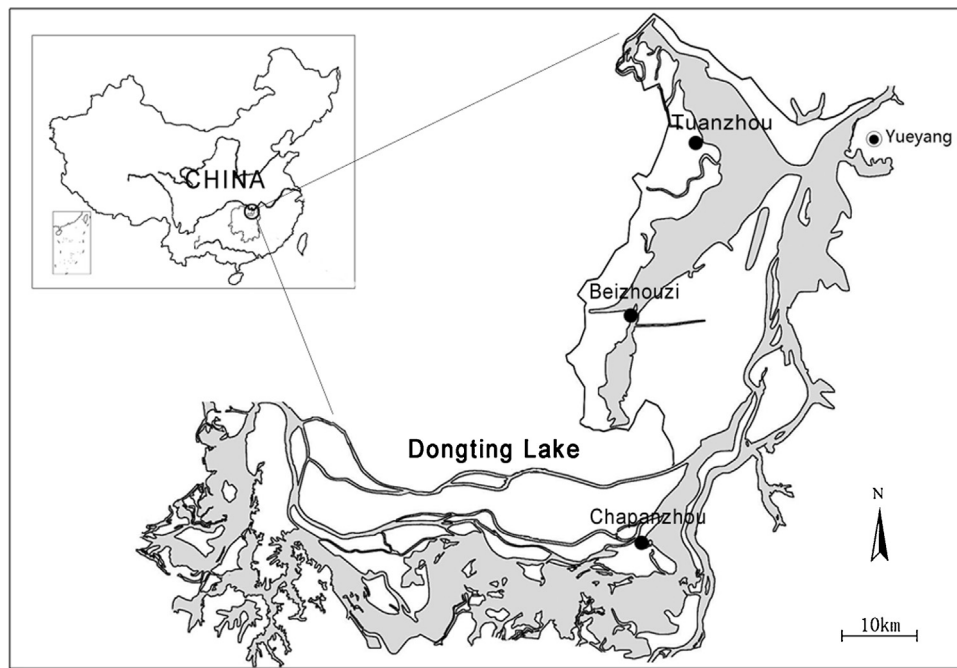


Fig. 1. Locations of the sampling sites in the Dongting Lake wetlands, China.

excavated from each sampling point, providing a total of 15 sampled quadrats per species per sampling date. In each quadrat, all ramets within the sampling frame were counted and clipped. A preliminary study indicated that most rhizomes of the four species are distributed within the top 10 cm of soil. Using a shovel, we excavated the soil within each frame to a 15 cm depth to ensure that all the rhizomes were collected. Each collected sample was placed in a plastic bag and taken to the laboratory. Samples were collected in early November 2010 (approximately 1 week after the flood waters receded), mid-January 2011 (the coldest month), early March 2011 (after the spring sprout), and early May 2011 (before flooding).

2.4. Sample processing

We used tap water to carefully clean soil from the roots, and then separated the rhizomes in each quadrat. Belowground buds (rhizome meristems) were examined under a microscope and counted. Only developed meristems that formed a distinct stem tissue bud were counted (Dagleish and Hartnett, 2006). Bud bank density was calculated as the number of buds per m². The ratio of belowground buds to aboveground shoots can be used as an index of meristem limitation, with values of less than one indicating meristem limitation (Benson et al., 2004; Dagleish and Hartnett, 2006).

2.5. Data analysis

The differences in bud and shoot density among the four macrophyte species and among seasons were analyzed using mixed linear models, with species and season as the main factors, and sample site included as a random factor (McKone and Lively, 1993). For each species, a linear regression was performed to examine the relationship between the density of newly emerging shoots in March and the density of belowground buds in January. Because the sprouting of *P. hydropiper* shoots in Chapanzhou was later than in the other two sites, the respective five quadrats for this species were not included in the regression analysis. A least squares linear regression was performed to examine the relationship between peak bud density and elevation, using species as the experimental unit. The

peak bud density of each species was calculated as the mean of the 15 quadrats taken from the three sites in winter. 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. All statistical analyses were performed using the statistical software SPSS V15.0 (SPSS Inc., USA).

3. Results

3.1. Peak bud density among species and its relationship to elevation

Regression analysis revealed a significantly decreasing linear relationship between peak bud density and elevation (Fig. 2). Elevation alone explained 85% of the variability among the peak bud density of the four species (Fig. 2). Pair-wise comparisons indicated that *P. arundinacea* had the largest bud banks with a peak

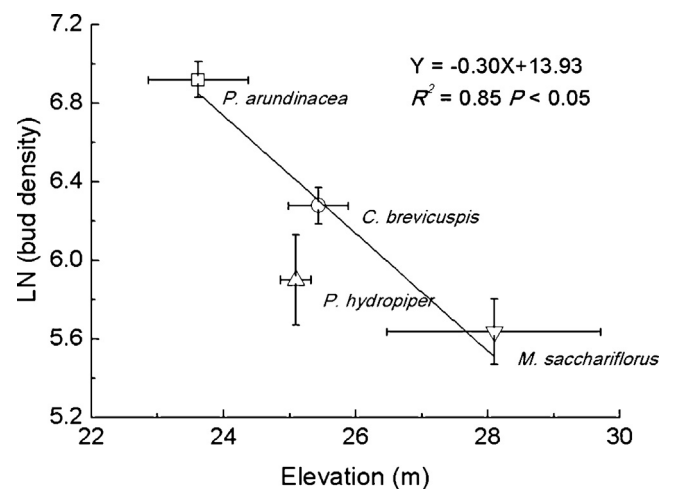


Fig. 2. Relationship between peak bud bank density and average elevation in the Dongting Lake wetlands. Symbols represent the mean bud density of each species in January ($n_{\text{studysites}} = 3$, $n_{\text{samplingquadrats}} = 15$), error bars: ± 1 SE.

Table 2

Two-way ANOVA of bud density and shoot density with species and season as main factors. The percentage of variance explained (SS%) and the level of significance (*P*) are presented.

Variable	Species (Sp)		Seasons (Se)		Sp × Se	
	SS%	<i>P</i>	SS%	<i>P</i>	SS%	<i>P</i>
Bud density(buds/m ²)	27.7	0.000	30.5	0.000	9.7	0.000
Shoot density(shoots/m ²)	84.1	0.000	1.6	0.000	2.9	0.000
d.f.	3		3		9	

bud density of 1049 ± 70 buds m⁻² (in January). The bud densities of *C. brevicuspis* and *P. hydropiper* were not significantly different, but were both lower than the bud density of *P. arundinacea* (*C. brevicuspis*, 565 ± 52 buds m⁻²; *P. hydropiper*, 484 ± 78 buds m⁻²). *M. sacchariflorus* had significantly smaller peak bud banks (333 ± 52 buds m⁻²) than *P. arundinacea* and *C. brevicuspis*, but these did not differ significantly from the bud banks of *P. hydropiper* (Fig. 2).

3.2. Seasonal patterns of bud bank and shoot density

From November 2010 to May 2011, bud bank density varied significantly among species and among seasons, with a significant interaction between species and season ($P < 0.001$; Table 2). All species, except *M. sacchariflorus*, exhibited similar seasonal patterns in the bud bank: density peaked in January, decreased markedly in March, and was lowest in May. In contrast, the bud density of *M. sacchariflorus* remained relatively constant (269 – 332 buds m⁻²), and only decreased significantly in May (178 ± 30 buds m⁻², $P < 0.05$; Fig. 3A). Among the four study species, *P. arundinacea* had the highest bud bank density during the growing season. However, the species having the lowest bud density differed among

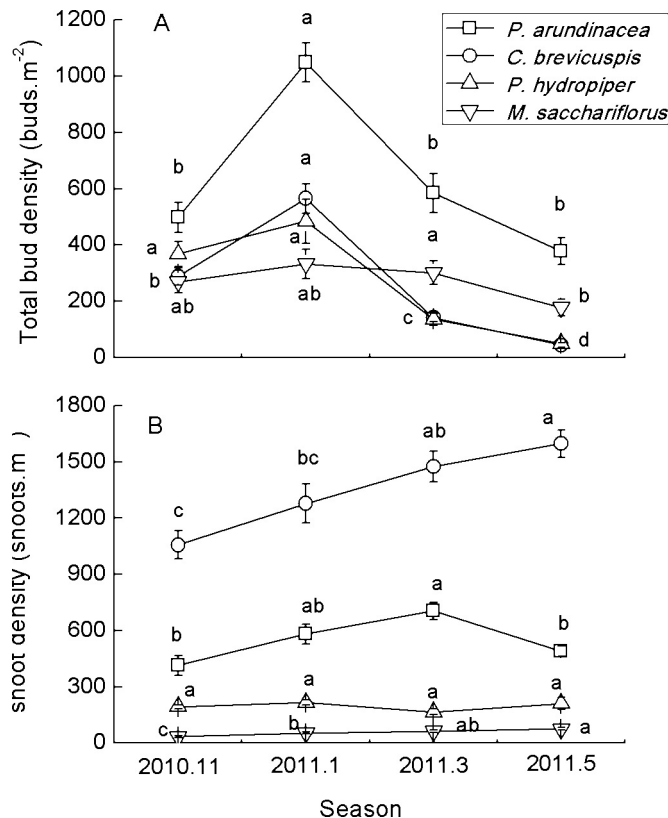


Fig. 3. Belowground bud bank density (A) and shoot density (B) of the four dominant macrophytes across seasons in the Dongting Lake wetlands. Different letters indicate differences at the 0.05 significance level ($n = 15$, Tukey test).

seasons: *M. sacchariflorus* and *C. brevicuspis* in November; *M. sacchariflorus* in January; and *C. brevicuspis* and *P. hydropiper* in March and May (Fig. 3A).

Shoot density varied significantly among species and among seasons, with a significant interaction between species and season ($P < 0.001$; Table 2). Shoot density was consistently highest for *C. brevicuspis* and lowest for *M. sacchariflorus* ($P < 0.05$; Fig. 3B). The shoot density of *P. arundinacea* and *C. brevicuspis* peaked in March; whereas, that of *M. sacchariflorus* and *P. hydropiper* peaked in May (Fig. 3B).

3.3. Relationship between shoot and bud density

For each species, regression analysis revealed a significant positive relationship between newly emerging shoots in March and bud density in January (Fig. 4). The meristem limitation index value of *C. brevicuspis* was 0.35, indicating meristem limitation; whereas, the indices for *P. arundinacea*, *P. hydropiper*, and *M. sacchariflorus* were greater than one (1.49, 2.24, and 4.38, respectively).

4. Discussion

Low-elevation *P. arundinacea* had a larger bud bank than high-elevation *M. sacchariflorus* over the whole growing season, which supports our first hypothesis. In lake wetlands connected to rivers, fluvial disturbances in the form of water level fluctuations and scouring affect all plant communities, but with varying frequency, amplitude, and predictability. The low-elevation *P. arundinacea* is more frequently impacted by flooding than other plant communities, and may thus benefit from a large bud bank for rapid regeneration after flooding disturbances. In contrast, *M. sacchariflorus* is less frequently impacted by flooding due to its high-elevation distribution and tall stature. Most stems of *M. sacchariflorus* can survive during the flooding season without the need for resprouting after flooding, like *P. arundinacea* and *C. brevicuspis*. In addition, the buds of *M. sacchariflorus* are considerably larger than those of the other three species (Deng et al., 2013b), which is probably associated with a higher production cost (Vesk and Westoby, 2004). *M. sacchariflorus* may benefit from a small bud bank because of the low probability of disturbance and the high production cost.

The bud bank density of *C. brevicuspis*, *P. hydropiper*, and *P. arundinacea* peaked in winter and decreased markedly after the spring sprout; whereas, that of *M. sacchariflorus* did not decrease significantly after the spring sprout. This finding only partially supports our second hypothesis. For *P. arundinacea*, *P. hydropiper*, and *C. brevicuspis*, it is likely that the majority of buds sprouted to recruit shoot populations in the spring; consequently, few new buds were recruited into the bud bank after the spring sprout. For *M. sacchariflorus*, it is likely that only a small proportion of buds sprouted to recruit the shoot population in the spring, and therefore the majority of buds remained dormant even after the spring sprout (the bud to shoot ratio was 4.38). *M. sacchariflorus* may make gradual and continual deposits to the bud bank after shoot emergence, perhaps creating a continuously available propagule pool (Dalgleish and Hartnett, 2006).

For *C. brevicuspis*, *P. hydropiper*, and *P. arundinacea*, the bud bank size available for regeneration is small after the spring sprout, indicating these three species are sensitive to the timing of disturbance (Huhat et al., 2000; Klimešová and Klimeš, 2007). During the growing season, irregular flooding caused by regional precipitation can submerge the low elevation-distributed vegetation for weeks, and therefore probably causes death of the shoot population. After re-emergence, these species may not have a sufficient bud bank to completely replace the aboveground shoot population. In

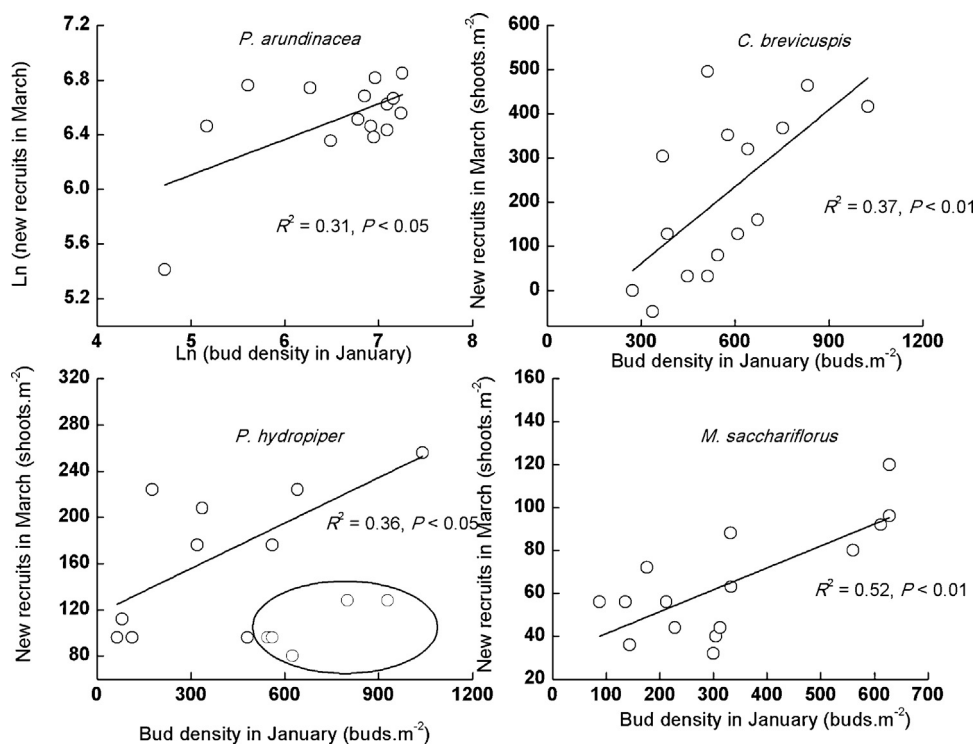


Fig. 4. The relationship between the density of belowground bud banks and the density of newly emerging shoots in March in the Dongting Lake wetlands. For *P. hydropiper*, the five quadrats in Chapanzhou (in the circle) were not included in the analysis.

addition to flooding, cattle grazing can reduce shoot populations in the Dongting Lake wetlands during the growing season. Increased tillering from the bud bank is an important source of resilience to herbivory (N'Guessan and Hartnett, 2011). A small bud bank size may constrain the capacity of these three species to compensate for biomass loss through increased tillering after the spring sprout (Huhat et al., 2000). In particular, *C. brevicuspis* may not have a sufficient number of buds present in the bud bank during the growing season to completely replace the aboveground shoot population (the meristem limitation index was 0.35), which suggests that this species may be vulnerable to disturbances such as heavy grazing. In contrast, *M. sacchariflorus* may be less sensitive to the timing of disturbance, because it can rely on a consistently available bud bank. Further research is needed to clarify the relationship between bud bank availability and population resilience after disturbance in these species.

It is noteworthy that bud bank densities for all four species were lowest in May which is just before flooding. *C. brevicuspis* and *P. arundinacea* flower and fruit from April to May in the Dongting Lake wetlands. During this period, energy and nutrients may be allocated to inflorescence development rather than to new rhizome formation (Bernard, 1990; Chen et al., 2014a). However, *M. sacchariflorus* and *P. hydropiper* normally flower and fruit after flooding from October to November (Deng et al., 2013b). The Dongting Lake wetlands experience a long flooding season from June to October. Maintenance of a large bud population through the long flooding season would incur significant metabolic costs (Lehtila and Larsson, 2005; Chen et al., 2014a). A small meristem population before flooding might therefore be a strategy to reduce maintenance costs through the flooding season.

Dalgleish and Hartnett (2006) suggest that among grassland ecosystems, those with relatively large belowground bud banks may be the most resilient to environmental change. The bud bank density of *P. arundinacea* was the highest among the four species examined, which suggests that this species may have developed

a large regeneration capacity in response to changes in the flooding regimes of Dongting Lake that have occurred since operation of the Three Gorges Reservoir started in 2003 (Ou et al., 2012; Lai et al., 2013). Furthermore, the concentrations of nutrients, particularly nitrogen and phosphorus, have increased markedly in many lake wetlands in recent decades (Chuai et al., 2012). *P. arundinacea*, with a large bud bank, may benefit more from this nutrient enrichment than species with smaller bud banks (Knapp and Smith, 2001; Dalgleish and Hartnett, 2006).

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