Original Article

Differences in belowground bud bank density and composition along a climatic gradient in the temperate steppe of northern China

Jianqiang Qian¹,², Zhengwen Wang¹, Jitka Klimešová², Xiaotao Lü¹, Wennong Kuang¹, Zhimin Liu¹*, Xingguo Han¹

¹CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110164, P. R. China,
²Department of Functional Ecology, Institute of Botany ASCR, CZ-379 82 Třeboň, Czech Republic,
*For Correspondence.

Running Title: Belowground bud bank along a climatic gradient in temperate steppe

Corresponding author

Zhimin Liu

Institute of Applied Ecology, Chinese Academy of Sciences,
72 Wenhua Road,
Shenyang 110016,
P. R. China.
Email: zmliu@iae.ac.cn
**Background and Aims** Understanding the changes in belowground bud bank density and composition along a climatic gradient is essential to explore species distribution pattern and vegetation composition in response to climatic changes. Nevertheless, investigations on bud banks along climatic gradient are still scarce. We expect that bud banks would be reduced in size in arid conditions and costly, bud-bearing organs with long spacers would be replaced by more compact forms with better protected buds than those found in moist conditions.

**Methods** We tested how total bud density and composition (different bud bank types) change with aridity (calculated value: 0.43-0.91), mean annual precipitation (MAP: 93-420 mm) and mean annual temperature (MAT: -1.51-6.93 °C) at 21 sites along a 2500 km climatic gradient in the temperate steppe of northern China.

**Key Results** The relationship between belowground bud bank density and precipitation/aridity was fundamentally changed along the climatic gradient, i.e., bud bank density increased first and then decreased along the aridity and MAP gradients with the turning points were aridity=0.67 and MAP=260 mm, respectively, while it decreased consistently with increasing MAT. The proportion of the bud bank that were tiller buds or dicotyledonous herb buds fluctuated along the aridity gradient. The proportion of rhizome buds was higher at relatively moist sites (aridity<0.75), while that of bulb buds was higher at drier sites (aridity>0.75).

**Conclusions** Belowground bud bank density decreases towards the dry, hot end of the climatic gradient. Based on the distribution of bud types along the climatic gradient, bulb buds and tiller buds of tussock grasses seem to be more resistant to environmental stress than rhizome buds. The dominance of annual species and smaller bud bank in arid region implies that plant reproductive strategies and vegetation composition will be shifted in scenarios of increased drought under future climate change.

**Keywords**: adaptive strategy, aridification, climate change, clonal traits, community dynamics, precipitation gradient
INTRODUCTION

Angiosperms originally evolved in moist and shady habitats, but later spread to other ecosystems as the climate started to be drier and/or colder (Field et al., 2009; Zanne et al., 2014). Among angiosperms, herbaceous species largely avoid harsh climate by senescing aboveground tissues and persisting through adverse seasons belowground in the form of dormant, bud-bearing organs (Raunkiaer, 1934; Zanne et al., 2014). This strategy enables perennial herbs to dominate vast ecosystems characterized by dry and/or cold periods and, moreover, to thrive in the face of various disturbances such as fire or grazing (Benson et al., 2004; Klimešová and Klimeš, 2007; Dalgleish and Hartnett, 2009; Zhao et al., 2013). In ecosystems dominated by perennial herbs, such belowground bud banks are known to provide buffering that effectively resists short-term climatic perturbations (Hoover et al., 2014; Vanderweide and Hartnett, 2015). In particular, herbaceous communities with large bud banks have the potential to respond quickly to disturbance, increased nutrient availability or precipitation (Hartnett et al., 2006; Dalgleish et al., 2008; Dalgleish and Hartnett, 2009; Zhao et al., 2010) and therefore are resilient in response to short-term perturbations (Dalgleish et al., 2012; Yin et al., 2013; Vanderweide et al., 2014; Wu et al., 2014). However, long-term climatic changes may show their negative influences on these plants (Clark et al., 2002; Yin et al., 2013).

While previous research has demonstrated that long-term drought conditions could drive the large and widespread decline of perennial species (McAuliffe and Hamerlynck, 2010), the role of bud banks in perennial vegetation dynamics has been rarely explored. Indeed, bud banks are known to be affected by disturbances (Fidelis et al., 2014; Herben et al., 2016), and their diminishment in response to drought (Carter et al., 2012; Vanderweide and Hartnett, 2015) and cryoturbation (Klimešová and Doležal, 2011; Klimešová et al., 2012) have been documented. Thus, the increased frequency and intensity of such extreme weather phenomena as the heat
waves and long-term drought (Piao et al., 2003; Smith et al., 2011; Dai, 2013; Yin et al., 2013) projected to result from contemporary climate change would pose particular challenges for communities that rely on such bud banks. For example, the annually burned tallgrass prairie of North America is particularly reliant on the belowground bud bank, with more than 99% of its aboveground shoots seasonally recruited from it, whereas the contribution of soil seed bank is negligible (Benson and Hartnett, 2006). Moreover, experimental drought has been found to temporarily reduce prairie bud bank (Vanderweide and Hartnett, 2015) – which should raise concern about the impacts of likely long-term drought. In particular, prairies at the dry end of the precipitation gradient across North America were found to have very small bud banks where annual plants recruiting from seed bank play a major role beside recruits from bud bank (Dalgleish and Hartnett, 2006). For some perennial herbaceous plants (e.g. Bouteloua gracilis in the mixed prairie of North America), even though the vegetative regeneration rate is low, vegetative regeneration is still an important strategy in their life history, and periods of extreme climatic conditions (i.e. prolonged drought) may have important effects on population demography (Fair et al., 1999). The effect of climatic variations on seed germination and seedling establishment has proved to contribute to the shift in species dominance pattern under predicted climatic changes (Peters, 2000). VanderWeide et al. (2014) also confirmed that multi-years’ growing-season drought has no effects on belowground bud density, but changes the plant community structure in tallgrass prairie. Thus, long-term drought might be expected to cause the shift in plant reproductive strategies and changes in vegetation composition.

The responses of herbaceous community bud banks to dry conditions depend not only on bud number but also on other bud bank traits. In particular, some bud-bearing organs are better adapted to dry conditions than others. For example, bulbs, which are actually large buds that protect apical meristems with thickened scale leaves or leaf bases, contain stored water, and are especially suited to periodically dry climates (Pate and Dixon, 1982). Similarly, due to
intravaginal tillering, buds located at tiller bases of graminoids (epigeogenous rhizomes *sensu* Klimešová and Klimeš, 2008) are protected by leaf sheaths and are known to prefer dry habitats (Klimeš *et al.*, 1997, Klimešová *et al.*, 2011, 2012). In contrast, belowground rhizomes (hypogeogenous rhizomes *sensu* Klimešová and Klimeš, 2008) avoid dry places with undeveloped soil (Klimeš, 2003, 2008, Klimešová *et al.*, 2011, 2012). On the other hand, climate-induced changes in the distribution of bud-bearing organs along aridity gradient may have vast consequences, as the bud-bearing organs affect ecosystem services such as carbon sequestration (Cornelissen *et al.*, 2014; Ye *et al.*, 2015), biomass production (Vanderweide and Hartnett, 2015) and soil protection against wind erosion (Liu *et al.*, 2012). Thus, although bulbs and tiller bases should be more adapted to aridity, they do not provide very good soil protection against wind erosion due to their poor clonal spread (bulbs) or clumped growth form (tussock-grass tillers). Moreover, these two bud-bearing organs differ in their multiplication possibilities, as bulbs usually produce only one or a few offspring bulbs (Irmish, 1850), whereas tiller bases contain numerous reserve buds (Ott and Hartnett, 2015a). Long hypogeogenous rhizomes, which not only are the best belowground organs at protecting soil against wind erosion (Liu *et al.*, 2012) but also contribute to carbon sequestration (Cornelissen *et al.*, 2014), are – in contrast to bulbs and tiller bases – especially sensitive to drought. Moreover, hypogeogenous rhizomes usually do not use their buds for seasonal regrowth (Ott and Hartnett, 2015b).

In the present study, we sought to evaluate the potential constrains to vegetation response to climatic changes along an aridity gradient of the grassland biome of Inner Mongolia, China. We did this by assessing the belowground bud bank densities with respect to bud-bearing organs at 21 sampling sites along a 2500 km transect. Due to the regional temperate continental monsoon climate, it features a climatic gradient from wet, cold climate in the east to dry, hot climate in the west. Using this environmental gradient, we aimed to test the following two hypotheses: (1)
belowground bud bank density will decrease towards the dry, hot end of the gradient; and (2) the proportion of buds better protected (bulbs, grasses shoot bases) will increase whereas the proportion of buds located on rhizomes will decrease in the same direction.

**MATERIALS AND METHODS**

**Study sites**

The study was conducted in the temperate steppe of northern China (Inner Mongolia). This habitat has long-term been used for moderate grazing, but land degradation and desertification have occurred in some areas due to overgrazing and other inappropriate uses during past decades (Yang et al., 2005; Briske et al., 2015). The climate is seasonal, and plants are active in the warm period from April to September and dormant in winter. The longitudinal range of the 21 sampling sites is 104.45°-120.36° E, the latitudinal range is 40.73°-49.88°N, and the elevation range is 534-1518 m a.s.l. (Fig. 1; Table 1). From west to east, three types of vegetation were investigated: (i) desert steppe (approximately study sites 1-10, MAP: 93-204 mm), with sparse occurrence of low shrubs *Nitraria, Suaeda, Ephedra* and *Reaumuria*, accompanied by *Allium* species and grasses such as *Stipa breviflora* Griseb. and *Cleistogenes squarrosa* (Trin.) Keng, with productivity about 8-55 g/m²; (ii) typical steppe (approximately study sites 11-12 and 16-18, MAP: 222-297 mm), with productivity c. 30-160 g/m²; and (iii) meadow steppe (approximately study sites 13-15 and 19-21, MAP: 324-420 mm), as similar with the typical steppe, dominated by *Leymus chinensis* (Trin.) Tzvel. and *Agropyron cristatum* (Linn.) Gaertn, as well as by similar species from the genera *Stipa, Carex*, and *Cleistogenes*, but with higher productivity about 130-170 g/m². The plant species richness increased from 5 to >25 species per m² from west to east on this temperate steppe.

**Climate data collection**

We used three parameters to describe the climatic gradient: mean annual precipitation (MAP),
mean annual temperature (MAT) and aridity. Using these multiple variables enables us to both
compare our data with a few relevant published studies that use one or more of them, and
moreover to disentangle the potential contributions of each of these variables to the observed
bud bank patterns. The MAT and MAP data (1950-2000) were extracted from a global climate
dataset with a resolution of 0.0083×0.0083 (approximately 1 km² at the equator), obtained from
http://www.worldclim.org. The potential evapotranspiration (PET) data (1950-2000) were
extracted from the CGIAR-CSI Global Aridity Index and Global Potential Evapo-Transpiration
to east along the transect, MAP increased while MAT decreased, so the aridity was used to
incorporate MAP and MAT into one parameter to assess the changes of belowground bud bank
along the gradient, because PET is strongly determined by MAT. The aridity in this study was
defined as 1-MAP/PET (MAP/PET was used in several studies as Aridity Index, e.g.
Delgado-Baquerizo et al., 2013; Luo et al., 2016; we do not use this measure as its value is
increasing with increasing wetness of the climate). Thus the higher value of aridity indicates the
more serious water stress along the gradient.

Belowground bud bank sampling

During and just after the sexual reproduction stage (flowering and/or fruiting) of plant
communities on the temperate steppe, belowground bud banks were sampled during the period
from Jul. 30 to Aug. 14, 2012. The phenological difference was relatively negligible during the
sampling period, and the result from the analysis using sampling date as a covariate indicated
that sampling date had no significant effect on bud density. Sampling locations were
GPS-referenced in terms of latitude, longitude and elevation (±3 m accuracy, eTrex Venture,
Garmin, USA).

Sampling sites (21 in total) were placed almost evenly to characterize the whole climatic
gradient and to avoid grasslands degraded due to inappropriate management. All sampling sites
could represent semi-natural communities lacking significant human perturbation. At each sampling site, two 50 m×50 m plots (about 1 km apart from each other) were established. In each plot, five 1 m×1 m quadrats (at the center and in the four corners) were selected to investigate the vegetation coverage and the species composition and biomass of aboveground plant communities. Nearby each vegetation quadrat, one soil core (20 cm×20 cm×20 cm) along with the aboveground shoots arising from it was excavated. The connections between aboveground shoots and belowground organs were kept intact for subsequent species and bud type identification of the belowground bud bank. Soil block also contained fragments of bud bearing organs without above-ground parts which reached sampled plot from the side; we did not observe dormant belowground organs lacking aboveground shoots. Thus, at each sampling site, 10 soil cores/belowground bud bank samples were taken. The soil was carefully removed from the plant material, and all samples were placed in plastic bags and transported to a laboratory and stored in an incubator (4 °C) before bud identification and counting. All samples were processed within two weeks, and no rotting occurred during this period. Only turgid bud tissue was counted, with necrotic or visibly dead tissue discarded. We defined four types of bud banks, according to the morphological characteristics of bud-bearing organs: tiller buds (axillary buds at the shoot bases of caespitose species and rhizomatous grasses), rhizome buds (axillary buds and apical buds on the hypogeogenous rhizomes), bulb buds (meristems wrapped in the swollen base of bulb-type species) and buds on belowground parts of dicotyledonous herbs (comprising diverse organs such as short hypogeogenous rhizomes, epigeogenous rhizomes and roots capable of adventitious sprouting, but all bearing simple buds not protected by specialized organs), which we hereafter refer to as “dicot buds”. Buds on rhizomes and roots could be counted directly, whereas shoot bases needed to be dissected for tiller bud and bulb bud counting.

Data analysis
The original dataset of bud densities was converted into numbers of buds per m$^2$. The average bud density of each sampling site was then calculated for further analysis. The stepwise multivariate regression was used to relate total bud density to environmental variables MAT, MAP, aridity, PET and altitude. From the distribution pattern of study sites, we noted that the east end of the transect turns to northeastward (9 sites), and according to the preliminary analysis, the relationship between bud density and climatic variables (MAP and aridity) was fundamental changed for the two parts of the transect, so stepwise multivariate regressions were also conducted to analyze the relationships between environmental variables and total bud densities for the south-west 12 sites and north-east 9 sites separately. In addition, regression analysis were conducted to explore the changes in total bud densities and those of each bud bank type along the MAT, MAP and aridity gradient. The regression types, $R^2$ values and ANOVA tests of probabilities of significance were calculated using the regression curve-fit routine in SPSS package. The statistical analyses were performed using SPSS 18.0 (SPSS Inc., USA). Differences were considered significant at the level of $p<0.05$.

RESULTS

**Relationships between total bud densities and environmental variables**

Based on the results of stepwise multivariate regressions, among the five selected enviromental variables (MAT, MAP, aridity, PET and altitude), MAT explained 65% variations in total bud density along the whole transect ($p<0.01$). As the east end of our transect turns to northeastward, we analyzed the relationships between total bud densities and environmental variables for the first 12 sites and the later 9 sites separately. Our results showed that for the west part of the transect (12 sites), aridity explained 60% variation in total bud density ($p<0.05$), while for the east part of the transect (9 sites), MAP explained 37% variation in total bud density ($p<0.05$) (Table 2).
Changes in total bud density along the climatic gradient

In the temperate steppe of northern China, total bud density decreased consistently with increasing MAT ($p<0.01$, Fig. 2a). However, the relationship between bud bank and precipitation/aridity was fundamentally changed along the climate gradient. Along the precipitation gradient, total bud density first increased (from 105±45 bud/m$^2$ to 873±147 bud/m$^2$; $p<0.05$) and then decreased significantly (from 3133±330 bud/m$^2$ to 928±177 bud/m$^2$; $p<0.05$) with a turning point around MAP=260 mm, and the total bud density at the moist end was higher than that at the arid end of the gradient (Fig. 2b). Meanwhile, along the aridity gradient, total bud density first increased and then decreased significantly ($p<0.05$) with a turning point about aridity=0.67. Similarly, compared with the total bud density at the moist end, the arid end of the gradient harbored smaller bud density (Fig. 2c).

Changes in bud bank composition along the climatic gradient

The proportions of tiller buds and buds of dicotyledonous herbs of total bud density fluctuated along the aridity gradient. The proportion of rhizome buds was higher at relatively moist sites (aridity<0.75), while the proportion of bulb buds was higher at drier sites (aridity>0.75) (Fig. 3). Densities of all bud types except bulb buds decreased significantly ($p<0.01$) along the mean annual temperature gradient (Fig. 4). Of the four bud bank types, tiller bud density did not change significantly within the drier part of the gradient, but then sharply reached its peak at MAP of about 260 mm, then decreased significantly with increasing MAP at the moist end of the gradient. Rhizome buds and buds of dicotyledonous herbs occurred only where MAP was above 150 mm, and bud densities increased significantly ($p<0.05$) along the precipitation gradient. Bulb buds could be found along the whole gradient and their density did not show consistent changes (Fig. 5).

Changes in aboveground vegetation along the climatic gradient

Along the climatic gradient, the coverage of aboveground vegetation decreased significantly
(p<0.01) with the increasing aridity (Fig. 6a). As regard to vegetation composition along the gradient, the relative richness of annuals in aboveground vegetation increased significantly (p<0.01) with the increasing aridity (Fig. 6b) and the sites with higher aridity had higher biomass proportion of annuals in plant communities (Fig. 6c).

DISCUSSION

Along the 2500 km long climatic gradient in China, the temperate steppe's bud banks were characterized by the predicted pattern, with smallest bud bank and greatest relative proportion of buds protected by specialized leaf organs (i.e., leaf sheath or scale leaf) at the dry, hot end of the gradient. Indeed, with increasing amounts of precipitation and decreasing temperature, the number of buds increased and their protection evidently was less important. Based on the aboveground vegetation coverage, the relatively sparser vegetation at the driest end of the climatic gradient may contribute to its smaller belowground bud bank. Importantly, the smaller bud bank and the predominance of annual plants in arid region imply that plant reproductive strategies and vegetation composition will be shift under future aridification in the temperate steppe of China. Since bud banks of perennial vegetation can buffer the effects of drought on ecosystems, making it more resistant to increasing drought intensity (Ruppert et al., 2015), with the low bud density and the potential dominant of annuals, the arid end of gradient in the temperate steppe might be more prone to ecosystem degradation under climate changes.

Total bud density changes along the climatic gradient

In the temperate steppe of Inner Mongolia, precipitation (MAP) increases while temperature (MAT) decreases from west to east along the climatic gradient. To assess the changes in belowground bud bank along the climatic gradient, we also used their combined measure in the form of aridity (Holdridge, 1959, Zomer et al., 2008). Total bud density showed a piecewise relationship with the aridity in the present study, with the turning point aridity=0.67 and bud
density about 3100 buds per m$^2$. The total bud density at the drier sites was lower than that at the moist sites (100 versus 900 buds per m$^2$), supporting our first hypothesis, which yielded the prediction that bud bank density would decrease towards the dry end of the climatic gradient. Since the relative richness of annuals in plant communities increased along the aridity gradient and higher biomass proportion of annuals in the drier region (Table 1; Fig. 6), we speculated the lower bud densities at the arid end of gradient are partially attributed to the predominance of annuals in this region. Similarly, a piecewise linear relationship was seen in relation to the precipitation gradient, with the peak bud density at MAP=260 mm. In contrast, the decrease in total bud density was confirmed along the temperature gradient.

Our results are partially in agreement with the previous study by Dalgleish and Hartnett (2006), who compared bud banks along a gradient ranging from 269 to 960 mm of annual precipitation in the Great Plains of North America. They also found decreasing numbers of buds towards the dry end of the gradient, where the minimum bud density (about 100 buds per square meter) was recorded. Our minimal number of buds at the dry end of the gradient was also 100 buds, but the dry end of the Chinese gradient was drier (MAP only 93 mm) than that of the American one. In conditions of about 260 mm of precipitation per year (equal to the driest place on the American gradient) we found about 3000 buds per square meter and it represents the overall maximum recorded for our climatic gradient. These differences might be caused by the different latitudinal positions of the two gradients and therefore the warmer climate along the North American gradient: in our study area in China, the mean January (the coldest month) temperature ranges from -26.7 °C to -11.2 °C and the mean July (the hottest month) temperature ranges from 15.8 °C to 21.8 °C, whereas in North American tallgrass prairie, the mean temperature in January is -4 °C to 1.6 °C and mean temperature in July is 25.1 °C to 30.6 °C (Dalgleish and Hartnett, 2006). The colder climate in China alleviates the detrimental impact of low precipitation on vegetation.
The relatively lower numbers of buds towards the wet end of the climatic gradient may be connected with higher productivity and larger shoot size. This also leads to lower bud numbers per surface area as the same area may accommodate a higher number of small shoots or lower number of large shoots (i.e., corners rule. see for example Kleiman and Aarssen, 2007). It is worth noting that while the total number of buds per area decreased towards the wet end of the climatic gradient, the number of buds for individual bud-bearing organs categories was variable but not decreasing. This may be caused by the fact that 20 cm×20 cm was rather small for the productive sites and often it was dominated by only one type of bud-bearing organ (tiller buds).

In the present study, total bud densities decreased significantly with increasing MAT, and of the tested environmental variables, MAT explained the most variability in bud densities than others due to its consistent effects on buds on different bud-bearing organs (i.e., all buds except for bulb buds decreased significantly with increasing MAT). To date, we have found few data enabling comparison of the temperature effect on bud bank density between our study area and other regions. In alpine ecosystem, previous studies suggest that clonal growth and bud bank become more important with decreasing temperature (along with the increasing altitude) (Evette et al., 2009). There are also reports about seasonal effects of temperature on bud bank dynamics in wet meadows (e.g. Chen et al., 2015) which we cannot use for comparison as our study is based on snap shot data from summer period. In short term experiments with increased temperature conducted on *Leymus chinensis*, the dominant species in grasslands of northern China, the belowground bud bank was found to increase in response to simulated warming (Wang et al., 2010; Li et al., 2014), probably due to enhanced growth. Other studies devoted to responses of vegetation to warming usually highlight the connection of warming with dryness and the strong joint effect of these two parameters (De Boeck et al., 2016).

*Shifts in belowground bud bank composition along the climatic gradient*

As shown by their changing proportions along the climatic gradient, different bud bank types
prevailed in different climatic conditions. In particular, tiller buds and dicot buds could occur
along the whole gradient and the proportion of bulb buds at the dry end of the aridity gradient
was higher than that at moist sites, while rhizomes buds were concentrated at the moist end.
This is in accord with the second hypothesis’s prediction that the ratio of buds better protected
from drought would increase with increasing aridity in comparison to buds located on rhizomes,
which also indicates that bulbous species might be advantageous under water stressful
conditions. This pattern is consistent with habitat preferences of rhizomatous species for moist
portions of gradients in other regions (Klimeš, 2003, 2008, Klimešová et al., 2011, 2012). Thus,
in a short-term experiment in American prairies, studied taxonomic groups (differing also in
bud-bearing organs) responded differently to drought, although their particular responses (and
those of particular bud-bearing organs) showed differences from the observations in our much
drier ecosystem; there, dicotyledonous herbs and sedges were more sensitive to experimental
dryness than rhizomatous grasses (Vanderweide and Hartnett, 2015). The lack of consistency in
reactions of particular bud-bearing organs might be attributable to their specific responses
along the gradients or to differences in the species pools.

The dominance of tussock grasses and bulbous plants at the arid end of the gradient also
implies that even if perennial herbs relying on bud banks for regeneration are present there,
these plants have very limited lateral spread and ability to protect against soil erosion in
comparison with rhizomatous species dominating at the wet end of the gradient. Furthermore,
under future climatic scenarios, warming and drying are expected to be more severe compared
to historical records (Cayan et al., 2010), therefore exploring the trends of bud bank density and
composition along the climatic gradient might be crucial for predicting plant community
dynamics and ecosystem functioning.

Our method of bud bank determination has its limitations, we were able to count only
preformed buds on bud bearing organs and therefore potential bud bank sensu Klimešová and
Klimeš (2007) is underrepresented in our study. Potential bud bank concerns adventitious bud formation on roots and this may occur only after plant injury and therefore need to be examined experimentally.

In conclusion, in the temperate steppe of northern China, the belowground bud bank density decreases towards the dry, hot end of the climatic gradient and bulb buds and tiller buds of tussock grasses are more resistant to environmental stress than bud banks on rhizomes. Our study also demonstrated the paramount effects of temperature on the belowground bud bank in the temperature steppe. From the perspective of vegetation regeneration, our study indicates that the changes in bud bank density and composition along the climatic gradient could be crucial to predict plant community composition and dynamics under future climatic scenarios.

ACKNOWLEDGEMENTS

We thank Jinlei Zhu, Haiyang Zhang, Kai Wei and Chao Wang for their assistance in field sampling and data analysis. We are indebted to Jonathan Rosenthal for his assistance in language editing. We also thank two anonymous reviewers for their valuable comments to improve the original version of this manuscript. This study was supported financially by the National Nature Science Foundation of China (41271529, 41371077 and 41501573), the Key Project of Chinese National Programs for Fundamental Research and Development (2013CB429905) and the Czech Science Foundation (project no. 14-36079G, Center of Excellence PLADIAS).


Hartnett DC, Setshogo MP, Dalgleish HJ. 2006. Bud banks of perennial savanna grasses in


Pate JS, Dixon KW. 1982. *Tuberous, cormous and bulbous plants*. *Biology of an Adaptive*
1 Strategy in Western Australia. Nedlands: University of Western Australia Press.
2
3 Peters DPC. 2000. Climatic variation and simulated patterns in seedling establishment of two
dominant grasses at a semi-arid-arid grassland ecotone. Journal of Vegetation Science 11:
4 493–504.
5
difference vegetation index (NDVI) in China from 1982 to 1999. Journal of Geophysical
7
8 Raunkiaer C. 1934. The Life Forms of Plants and Statistical Plant Geography. London:
9 Clarendon Press.
10
12 2015. Quantifying drylands' drought resistance and recovery: the importance of drought
13
14 Shi P, Yan P, Yuan Y, Nearing MA. 2004. Wind erosion research in China: past, present and
15
16 Smith MD. 2011. An ecological perspective on extreme climatic events: a synthetic definition
17
18 Vanderweide BL, Hartnett DC. 2015. Belowground bud bank response to grazing under
19
20 Vanderweide BL, Hartnett DC. Carter DL. 2014. Belowground bud banks of tallgrass
prairie are insensitive to multi-year, growing-season drought. Ecosphere 5: 103.
21
22 Wang JF, Gao S, Lin JX, Mu YG. Mu CS. 2010. Summer warming effects on biomass
23
24 Weaver JE, Albertson FW. 1936. Effect of the great drought of the prairies of Iowa, Nebraska
25


<table>
<thead>
<tr>
<th>Study site</th>
<th>Latitude(N)</th>
<th>Longitude(E)</th>
<th>Altitude</th>
<th>MAP</th>
<th>MAT</th>
<th>PET</th>
<th>Aridity</th>
<th>AGB</th>
<th>RRA</th>
<th>BPA</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>40.88</td>
<td>104.45</td>
<td>1461</td>
<td>93</td>
<td>6.12</td>
<td>983</td>
<td>0.91</td>
<td>7.93</td>
<td>32.86</td>
<td>30.21</td>
</tr>
<tr>
<td>2</td>
<td>40.73</td>
<td>105.61</td>
<td>1293</td>
<td>100</td>
<td>6.93</td>
<td>1025</td>
<td>0.90</td>
<td>45.17</td>
<td>31.92</td>
<td>17.33</td>
</tr>
<tr>
<td>3</td>
<td>41.80</td>
<td>107.47</td>
<td>1515</td>
<td>151</td>
<td>4.28</td>
<td>894</td>
<td>0.83</td>
<td>33.72</td>
<td>15.07</td>
<td>3.31</td>
</tr>
<tr>
<td>4</td>
<td>41.83</td>
<td>107.61</td>
<td>1513</td>
<td>156</td>
<td>4.11</td>
<td>890</td>
<td>0.82</td>
<td>48.75</td>
<td>12.68</td>
<td>1.19</td>
</tr>
<tr>
<td>5</td>
<td>41.91</td>
<td>108.71</td>
<td>1518</td>
<td>204</td>
<td>3.42</td>
<td>873</td>
<td>0.77</td>
<td>56.37</td>
<td>11.33</td>
<td>0.32</td>
</tr>
<tr>
<td>6</td>
<td>42.42</td>
<td>109.81</td>
<td>1151</td>
<td>180</td>
<td>5.22</td>
<td>937</td>
<td>0.81</td>
<td>28.67</td>
<td>20.90</td>
<td>10.41</td>
</tr>
<tr>
<td>7</td>
<td>42.93</td>
<td>110.82</td>
<td>1035</td>
<td>152</td>
<td>4.91</td>
<td>957</td>
<td>0.84</td>
<td>99.69</td>
<td>32.48</td>
<td>38.12</td>
</tr>
<tr>
<td>8</td>
<td>43.38</td>
<td>111.96</td>
<td>1013</td>
<td>148</td>
<td>3.56</td>
<td>921</td>
<td>0.84</td>
<td>46.56</td>
<td>40.72</td>
<td>38.74</td>
</tr>
<tr>
<td>9</td>
<td>43.63</td>
<td>112.20</td>
<td>956</td>
<td>147</td>
<td>3.50</td>
<td>921</td>
<td>0.84</td>
<td>54.17</td>
<td>42.27</td>
<td>53.47</td>
</tr>
<tr>
<td>10</td>
<td>43.71</td>
<td>112.92</td>
<td>1051</td>
<td>182</td>
<td>2.91</td>
<td>891</td>
<td>0.80</td>
<td>111.18</td>
<td>41.49</td>
<td>41.13</td>
</tr>
<tr>
<td>11</td>
<td>43.85</td>
<td>114.09</td>
<td>1050</td>
<td>222</td>
<td>2.16</td>
<td>872</td>
<td>0.75</td>
<td>94.88</td>
<td>40.74</td>
<td>50.79</td>
</tr>
<tr>
<td>12</td>
<td>43.98</td>
<td>114.83</td>
<td>1128</td>
<td>246</td>
<td>1.13</td>
<td>843</td>
<td>0.71</td>
<td>164.84</td>
<td>15.92</td>
<td>5.87</td>
</tr>
<tr>
<td>13</td>
<td>44.47</td>
<td>117.18</td>
<td>1048</td>
<td>324</td>
<td>1.03</td>
<td>818</td>
<td>0.60</td>
<td>133.17</td>
<td>10.93</td>
<td>0.29</td>
</tr>
<tr>
<td>14</td>
<td>44.99</td>
<td>118.75</td>
<td>987</td>
<td>380</td>
<td>0.83</td>
<td>809</td>
<td>0.53</td>
<td>153.24</td>
<td>13.08</td>
<td>2.91</td>
</tr>
<tr>
<td>15</td>
<td>45.43</td>
<td>119.72</td>
<td>972</td>
<td>420</td>
<td>0.42</td>
<td>788</td>
<td>0.47</td>
<td>164.51</td>
<td>15.29</td>
<td>2.91</td>
</tr>
<tr>
<td>16</td>
<td>48.09</td>
<td>118.46</td>
<td>718</td>
<td>285</td>
<td>-1.04</td>
<td>775</td>
<td>0.63</td>
<td>160.46</td>
<td>16.77</td>
<td>2.74</td>
</tr>
<tr>
<td>17</td>
<td>48.50</td>
<td>117.15</td>
<td>592</td>
<td>260</td>
<td>0.18</td>
<td>781</td>
<td>0.67</td>
<td>83.10</td>
<td>15.17</td>
<td>1.43</td>
</tr>
<tr>
<td>18</td>
<td>49.34</td>
<td>117.09</td>
<td>720</td>
<td>297</td>
<td>-1.49</td>
<td>740</td>
<td>0.60</td>
<td>157.21</td>
<td>33.79</td>
<td>17.50</td>
</tr>
<tr>
<td>19</td>
<td>49.78</td>
<td>118.53</td>
<td>534</td>
<td>332</td>
<td>-1.47</td>
<td>754</td>
<td>0.56</td>
<td>129.71</td>
<td>15.23</td>
<td>1.62</td>
</tr>
<tr>
<td>20</td>
<td>49.88</td>
<td>119.99</td>
<td>754</td>
<td>406</td>
<td>-1.51</td>
<td>712</td>
<td>0.43</td>
<td>173.70</td>
<td>9.11</td>
<td>5.80</td>
</tr>
<tr>
<td>21</td>
<td>49.19</td>
<td>120.36</td>
<td>632</td>
<td>392</td>
<td>-1.29</td>
<td>739</td>
<td>0.47</td>
<td>NA</td>
<td>11.07</td>
<td>NA</td>
</tr>
</tbody>
</table>

Note: MAP (mm) - mean annual precipitation, MAT (°C) - mean annual temperature, PET (mm) - potential evapotranspiration, Aridity (unitless), AGB (g per m$^2$) - aboveground biomass, RRA (%) - relative richness of annuals, BPA (%) - biomass proportion of annuals, NA - data not available.
TABLE 2. Results of stepwise multivariate regression for the relationships between total bud densities and environmental variables

<table>
<thead>
<tr>
<th>Independent variables</th>
<th>Total bud density (whole)</th>
<th>Total bud density (12 sites in the west)</th>
<th>Total bud density (9 sites in the east)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MAT</td>
<td>(-)**</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>MAP</td>
<td>...</td>
<td>...</td>
<td>(-)*</td>
</tr>
<tr>
<td>Aridity</td>
<td>...</td>
<td>(-)*</td>
<td>...</td>
</tr>
<tr>
<td>PET</td>
<td>...</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>Altitude</td>
<td>...</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>R²</td>
<td>0.65</td>
<td>0.60</td>
<td>0.37</td>
</tr>
</tbody>
</table>

Note: MAT (°C) - mean annual temperature, MAP (mm) - mean annual precipitation, Aridity (unitless), PET (mm) - potential evapotranspiration, Altitude (m). **p<0.01, *0.011<p<0.05.
**Figure Legends**

**Fig. 1** Distribution of sampling sites in the temperate steppe of northern China.

**Fig. 2** Changes in total bud bank density (mean±standard error) along the climatic gradient (mean annual temperature (a); mean annual precipitation (b); aridity (c)) in the temperate steppe of northern China.

**Fig. 3** Changes in the proportion (mean±standard error) of four different bud bank types (tiller buds (a); rhizome buds (b); bulb buds (c); and dicot buds (d)) across the aridity gradient in the temperate steppe of northern China.

**Fig. 4** Changes in bud densities (mean±standard error) of different bud bank types (tiller buds (a); rhizome buds (b); bulb buds (c); and dicot buds (d)) along the temperature gradient in the temperate steppe of northern China.

**Fig. 5** Changes in bud densities (mean±standard error) of different bud bank types (tiller buds (a); rhizome buds (b); bulb buds (c); and dicot buds (d)) along the precipitation gradient in the temperate steppe of northern China.

**Fig. 6** The changes in vegetation coverage (a), the relative richness (b) and biomass proportion (c) (mean±standard error) of annuals along the aridity gradient in the temperate steppe of northern China.
Fig. 1 Distribution of sampling sites in the temperate steppe of northern China.
Fig. 2 Changes in total bud bank density (mean±standard error) along the climatic gradient (mean annual temperature (a); mean annual precipitation (b); aridity (c)) in the temperate steppe of northern China.
Fig. 3 Changes in the proportion (mean±standard error) of four different bud bank types (tiller buds (a); rhizome buds (b); bulb buds (c); and dicot buds (d)) across the aridity gradient in the temperate steppe of northern China.
Fig. 4 Changes in bud densities (mean±standard error) of different bud bank types (tiller buds (a); rhizome buds (b); bulb buds (c); and dicot buds (d)) along the temperature gradient in the temperate steppe of northern China.
Fig. 5 Changes in bud densities (mean±standard error) of different bud bank types (tiller buds (a); rhizome buds (b); bulb buds (c); and dicot buds (d)) along the precipitation gradient in the temperate steppe of northern China.
Fig. 6 The changes in vegetation coverage (a), the relative richness (b) and biomass proportion (c) (mean±standard error) of annuals along the aridity gradient in the temperate steppe of northern China.