Ramet recruitment from different bud types along a grassland degradation gradient in Inner Mongolia, China

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ABSTRACT

Since the contribution of total belowground bud bank and different bud types to community regeneration has rarely been explored, the vegetative offspring recruited from different belowground bud types was investigated in four plant communities along a grassland degradation gradient in northeastern China (Inner Mongolia). This gradient, between 1000 and 1500 m a.s.l., has been caused by overgrazing. It is a *Leymus chinensis* steppe which occupies about 3.0×10^5 ha. Recruitment from tiller buds was dominant (>80%) in determining the total vegetative offspring density along the whole grassland degradation gradient. However, the proportional contribution of tiller-ramets to total ramet recruitment was significantly greater (P <0.05) during earlier than later stages of grassland degradation, while that of rhizome-ramets showed an opposite pattern. While the percentage contribution and density of root-derived ramets to total ramet density increased significantly (P <0.05) during the late stages of grassland degradation, those of bulb-ramets kept relatively constant along the whole grassland degradation gradient. The relative contribution of hemicryptophytes [i.e., *Achnatherum sibiricum, Cleistogenes squarrosa, Festuca ovina, Koeoleria cristata, Poa annua, Stipa grandis*] to total plant species richness decreased, while that of geophytes [i.e., *Agropyron cristatum, Carex korshinskyi. Leymus chinensis, Allium anisopodium, A. bidentatum, A. tenuissimum, Astragalus galactites, Cymbaria dahurica, Iris tenuifolin, Potentilla acaulis, P. bifurca, Pulsatilla turczaninovii, Serratula chinensis, Thalictrum aquilegifolium*] increased with the increases of grassland degradation. Our results showed that as grassland degradation increased, changes in the proportion of tiller-, rhizome- and root-derived ramets with respect to total ramet density determined in turn changes in the proportion of hemicryptophytes and geophytes in the study plant communities.

INTRODUCTION

Grassland degradation caused by overgrazing has been recognized as a major threat to ecosystem services and functioning, especially in arid and semi-arid regions (Mainguet 1994, Bai *et al.* 2007, Ford *et al.* 2012, Wiesmeier *et al.* 2012). The area of degraded grassland in China has reached approximately 1.35×10^8 ha. It accounts for one third of the available grassland area, and it increases at a speed of 2.0×10^6 ha yr^{-1} (Zhou and Wang 2002, Jia *et al.* 2006). Grassland degradation is usually accompanied by changes in plant community composition, then leading to changes in the vegetation succession process (Jauffret and Lavorel 2003, Wang *et al.* 2006). Since population regeneration plays important roles in determining plant community dynamics (Grubb 1977), understanding the dynamics of changes in population recruitment is essential to reveal the mechanisms of vegetation succession, and predict community dynamics.

Plant recruitment can be through sexual reproduction via seeds and/or vegetative reproduction via vegetative growth (Richards 1986). The trade-off between these two reproduction modes has been reported under different conditions (Eckert 2002). Seed dispersal or clonal growth traits have been accounted for community assemblage during the early or later phases of vegetation succession, respectively, along a human-made habitat degradation gradient in Europe (Latzel *et al.* 2011). Abiotic factors can be a major cause of grassland degradation, they can affect population regeneration or cause changes in population recruitment from different plant functional groups which possess specific reproduction types. Compared with soil seed bank, the belowground meristem population (the "bud bank" *sensu* Harper 1977) plays a more important role in population recruitment in some perennial, herbaceous communities. For instance, more than 99% of aboveground shoots are recruited from the belowground bud bank, while the soil seed bank plays a negligible role in tallgrass prairies of North America (Benson *et al.* 2004, Benson and Hartnett 2006). The dynamics in population recruitment via sexual regeneration along grassland degradation gradient has been extensively explored (Snyman 2004, Bossuyt and Honnay 2008). However, the contribution of vegetative regeneration via the belowground bud bank has rarely been discussed in plant communities along grassland degradation gradient.

Belowground bud banks can reflect the population regeneration in response to disturbances and environmental stresses, and be used for predicting community dynamics to some extent (Dalgleish and Hartnett 2006, 2009, Dalgleish *et al.* 2008, Zhang *et al.* 2009, Li and Yang 2011, Carter *et al.* 2012, Willand *et al.* 2013). However, even though the whole contribution of vegetative regeneration has already been discussed for some grasslands (Benson *et al.* 2004, Benson and Hartnett 2006), the relative regenerative contribution of different bud types has not been clarified to date. Klimešová and Klimeš (2007) reported that there are 17 types of clonal growth organs in the European flora, and that bud bank types can be defined according to the position, seasonality and function of clonal growth organs. Because of their differences in morphological characteristics and resource storage patterns (Vesk and Westoby 2004, Klimešová and Klimeš 2007), different bud types might respond or contribute differently to disturbances or population regeneration, respectively. Therefore, understanding the whole and the relative contribution of belowground bud banks to population regeneration is crucial to (1) explore the mechanisms leading to plant community dynamics, (2) predict changes in the community composition in the face of grassland degradation processes, and (3) implement adequate grassland management practices.

The present study aims to offer some valuable information on the contribution of different bud types to stem recruitment along a gradient of grassland degradation. Literatures reffering to the North American tallgrass prairie communities have primarily focused on differences in stem recruitment between forbs and grasses with different grazing and fire regimes (i.e., Benson and Harnett 2006, Dalgleish and Harnett 2009). In European grasslands, the literature has focused on bud bank traits of communities with different resource availabilities (i.e., Rusch *et al.* 2011) and stem recruitment of different bud types within a specific species (Bartušková and Klimešová 2010). This study adds to the growing literature on the bud sources of ramets within a community, and offers a perspective on the topic from eastern Asian grasslands and grasslands experiencing disturbance.

According to our previous field observation on belowground bud banks and their corresponding vegetative offspring, plant population regeneration at the beginning of the growing season is mainly accomplished through the sprouting of the belowground, overwintering bud banks in the study steppe. This is the result of increases in air and soil temperatures, and the arrival of adequate rainfall levels at the start of the season. Our observations were similar to findings of Dalgleish and Hartnett (2006) in their study on the tallgrass and mixed-grass prairies, short grass steppe and desert grassland across the central grassland of North America. They indicated that in arid grasslands, the majority of buds in

the bud bank quickly emerge into the year´s standing crop of stems. Therefore, we focused on the regenerative contribution of the belowground, overwintering bud banks at the beginning of growing season. We studied the vegetative offspring originated from different bud types in four plant communities along a grassland degradation gradient in a *Leymus chinensis* steppe of Inner Mongolia, China.

In the present study, we investigated (1) if the regenerative contribution from belowground, overwintering bud banks changed, and (2) what was the difference in the regenerative contribution from different bud types along that gradient. Answers to these questions are helpful to reveal and predict the plant community dynamics in the study temperate grassland, and implement an effective community management to reduce their degradation.

STUDY SITE

This study was conducted on the typical steppe nearby the Inner Mongolia Grass-

Table 1. Major species composition of plant communities along the grassland degradation gradient in a typical steppe of Inner Mongolia, China. Numbers from 1 to 4 indicate increased levels of grassland degradation.

| Levels of degradation			
1	2	3	4
Leymus chinensis (Trin.) Tzvel.	*Leymus chinensis* (Trin.) Tzvel.	*Leymus chinensis* (Trin.) Tzvel.	*Leymus chinensis* (Trin.) Tzvel.
Achnatherum sibiricum (Linn.) Keng	*Achnatherum sibiricum* (Linn.) Keng	*Achnatherum sibiricum* (Linn.) Keng	*Achnatherum sibiricum* (Linn.) Keng
Agropyron cristatum (Linn.) Gaertn.	*Agropyron cristatum* (Linn.) Gaertn.	*Agropyron cristatum* (Linn.) Gaertn.	*Agropyron cristatum* (Linn.) Gaertn.
Allium anisopodium Ledeb.	*Allium bidentatum* L.	*Allium bidentatum* L.	*Allium bidentatum* L.
Allium bidentatum L.	*Allium tenuissimum* L.	*Allium tenuissimum* L.	*Allium tenuissimum* L.
Allium tenuissimum L.	*Astragalus galactites* Pall.	*Artemisia frigida* Willd.	*Carex korshinskyi* Kom.
Artemisia sieversiana Ehrhart ex Willd.	*Carex korshinskyi* Kom.	*Artemisia sieversiana* Ehrhart ex Willd.	*Cleistogenes squarrosa* (Trin.) Keng
Axyris amaranthoides L.	*Chenopodium glaucum* L.	*Axyris amaranthoides* L.	*Iris tenuifolin* Pall.
Carex korshinskyi Kom.	*Cleistogenes squarrosa* (Trin.) Keng	*Carex korshinskyi* Kom.	*Koeoeria cristata* L.
Chenopodium glaucum L.	*Cymbaria dahurica* Linn.	*Chenopodium glaucum* L.	*Potentilla acaulis* L.
Cleistogenes squarrosa (Trin.) Keng	*Festuca ovina* L.	*Cleistogenes squarrosa* (Trin.) Keng	*Potentilla bifurca* Linn.
Cymbaria dahurica Linn.	*Koeoeria cristata* L.	*Cymbaria dahurica* Linn.	*Stipa grandis* P. Smirn.
Festuca ovina L.	*Poa annua* L.	*Iris tenuifolin* Pall.	*Thalictrum aquilegifolium* L.
Koeoeria cristata L.	*Stipa grandis* P. Smirn.	*Koeoeria cristata* L.	
Lappula myosotis V. Wolf	*Thalictrum aquilegifolium* L.	*Potentilla bifurca* Linn.	
Poa annua L.		*Salsoleae* C. A. Mey.	
Potentilla acaulis L.		*Serratula chinensis* S.Moore	
Potentilla bifurca Linn.		*Stipa grandis* P. Smirn.	
Pulsatilla turczaninovii Kryl. et Serg.		*Thalictrum aquilegifolium* L.	
Salsoleae C. A. Mey.			
Serratula chinensis S. Moore			
Stipa grandis P. Smirn.			
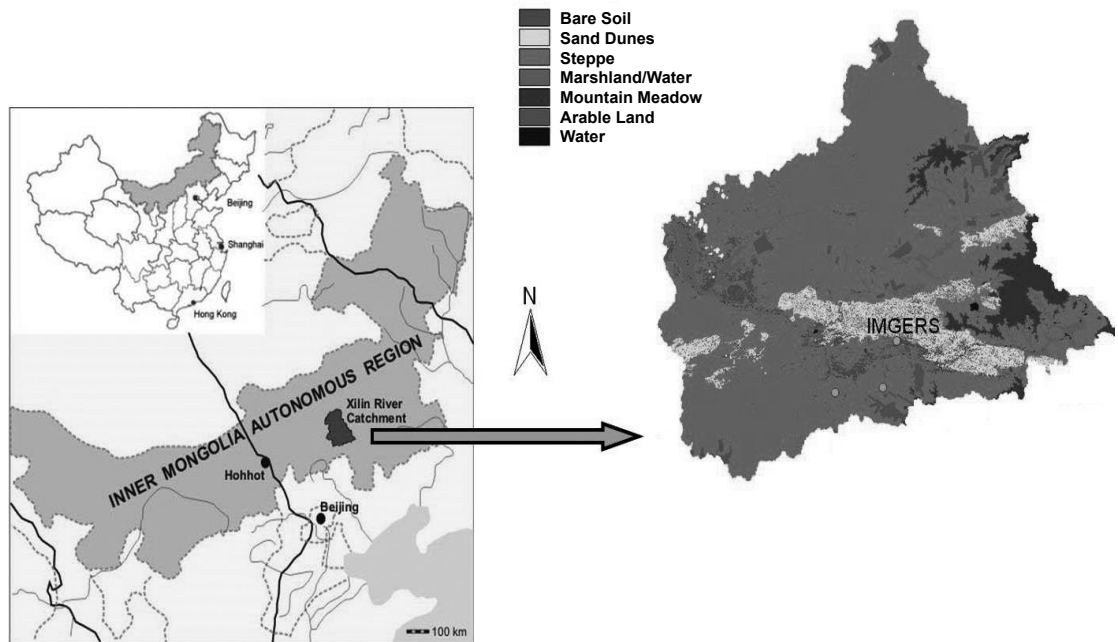
Fig. 1. Map of the study site. The Inner Mongolia Grassland Ecosystem Research Station (IMGERS), Chinese Academy of Sciences.

land Ecosystem Research Station (IMGERS, 43°38'N, 116°42'E, 1270 m a.s.l., Fig. 1), Chinese Academy of Sciences. The *Leymus chinensis* steppe, which occurs extensively in the temperate steppe of China and eastern Eurasia, occupies the largest area (about 3.0×10^5 ha) in the typical steppe of Inner Mongolia, China. During a long-term period, this steppe was exposed to grazing and mowing. Because of an inadequate utilization, it shows different levels of degradation now (Li *et al.* 1988, Bao *et al.* 2004, Tong *et al.* 2004). This has profound influences on the regional agriculture and animal husbandry production, since this typical steppe is one of the most important pastures in northern China.

The climate is semi-arid, continental and temperate. The mean annual precipitation is 335 mm (1982–2008), 60 to 80% of it falls as rainfall during the growing season (May to September). The mean annual temperature is 0.4°C. Mean monthly temperature ranges from –21.4°C in January to 19.0°C in July (1982–2008). Maximum values for precipitation and temperature typically occur during the period from June to August (Schönbach *et al.* 2011). Major soil types are calcic chestnuts and calcic chernozems (IUSS 2006).

MATERIAL AND METHODS

The study objects

The original vegetation was dominated by the perennial, rhizomatous grass *Leymus chinensis*; main companion species were *Stipa grandis*, *Cleistogenes squarrosa*, *Agropyron cristatum*, *Artemisia frigida* and *Carex korshinskyi* (Jia *et al.* 2006). The vegetation cover was about 30–40%, and could reach 70% in years with high precipitation (Bao *et al.* 2004). Although the study steppe was utilized for grazing and mowing during more than one thousand years (the long-term stocking rate on the study steppe is about 1.2 sheep units

ha^{-1}), grassland degradation caused by overgrazing occurred mainly in the past fifty years (Tong *et al.* 2006). Grassland degradation was uneven in the study area. As a result, the dominant species, and the plant community composition (and therefore the feeding attributes of the plant species) changed according to the intensity of the degradation process (Table 1). Based on the differences in plant community composition, productivity and resilience, Wu *et al.* (2011) defined four degradation grades along a grassland degradation gradient on the typical steppe of Inner

Mongolian Plateau, China. Xie and Wittig (2007) reported that increasing grazing intensity leads to a change in species composition and a reduction in the grazing potential of the community. *Artemisia* species, for example, are favored by high grazing intensity (Li 1989, Peer *et al.* 2001). Although total yield of rangeland vegetation is an indicator of forage resources, it does not indicate the food value of particular ranges to different animal users. The more important indicators of food value to different animal users partially include plant species composition and palatability. The number of forage species that comprises a particular pasture may be specially significant in rangelands like those in Mongolia (Damiran 2005). Palatability of plants should also be taken into account in order to estimate or monitor forage resources of the Mongolian rangelands correctly. Along the increasing grassland degradation mosaic, plant communities changed as indicated in Table 1; for example, at greater levels of grassland degradation, *Artemisia* species (which are hairy, highly sclerenchymatic and taste badly: Xie and Wittig 2007; plant community 3: Table 1), *Iris tenuifolia* (not consumable by sheep: Damiran 2005; plant communities 3 and 4: Table 1), and *Thalictrum aquilegifolium* (which migh be consumed but it is undesirable: Damiran 2005) were present. All these species were absent at the lowest study grassland degradation stage. In addition, it appeared to be a decrease in plant species richness at the greatest levels of grassland degradation (Table 1). Collins *et al.* (1986) reported that plant species richness decreased under increasing grazing pressure. Our objective was to determine the vegetative offspring

Table 2. Different bud bank types of various species in the *Leymus chinensis* steppe of Inner Mongolia, China. The family and life-form is indicated for each species.

| Bud bank types	Species	Family	Life-form
Tiller bud bank	*Achnatherum sibiricum*	Gramineae	hemicryptophyte
	Cleistogenes squarrosa	Gramineae	hemicryptophyte
	Festuca ovina	Gramineae	hemicryptophyte
	Koeoeria cristata	Gramineae	hemicryptophyte
	Poa annua	Gramineae	hemicryptophyte
	Stipa grandis	Gramineae	hemicryptophyte
Rhizome bud bank	*Agropyron cristatum*	Gramineae	geophyte
	Carex korshinskyi	Cyperaceae	geophyte
	Leymus chinensis	Gramineae	geophyte
Bulb bud bank	*Allium anisopodium*	Alliaceae	geophyte
	A. bidentatum	Alliaceae	geophyte
	A. tenuissimum	Alliaceae	geophyte
Root-derived bud bank	*Astragalus galactites*	Leguminosae	geophyte
	Cymbaria dahurica	Scrophulariaceae	geophyte
	Iris tenuifolin	Iridaceae	geophyte
	Potentilla acaulis	Rosaceae	geophyte
	P. bifurca	Rosaceae	geophyte
	Pulsatilla turczaninovii	Ranunculaceae	geophyte
	Serratula chinensis	Asteraceae	geophyte
	Thalictrum aquilegifolium	Ranunculaceae	geophyte
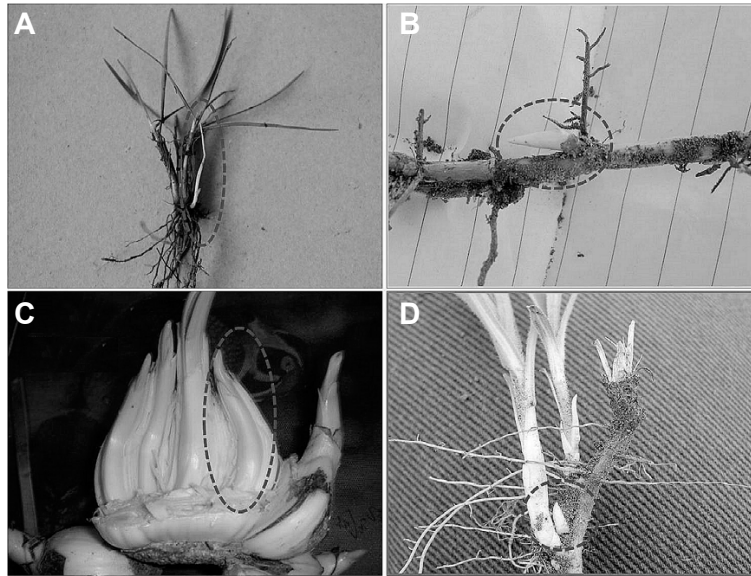
Fig. 2. Bud bank types. A: tiller buds; B: rhizome buds; C: bulb buds; D: root-derived buds. The dashed line highlights a young bud growing into a potential ramet.

recruited from different belowground bud types in the study grassland degradation gradient in northeastern China (Inner Mongolia). The dominant species on each of the four study plant communities as grassland degradation increased were *Leymus chinensis* + *Stipa grandis* + Perennial ruderals (community type 1); *Stipa grandis* + *Leymus chinensis* + Small bunch grasses (community type 2); *Artemisia frigida* + *Leymus chinensis* + Perennial ruderals (community type 3); and *Potentilla acaulis* + *Leymus chinensis* + *Stipa grandis* + Perennial ruderals (community type 4) (Table 1, see also Wu *et al.* 2011).

Experimental procedures

This investigation was conducted at the beginning of the growing season (late May) in 2012. According to our field investigation on belowground bud banks, more than 90% of the belowground, overwintering buds grow out into vegetative ramets at the beginning of growing season. Four plant communities of the *Leymus chinensis* steppe were selected for this study across an approximately 20 km grassland degradation gradient in Inner Mongolia.

Three plots (100×100 m each) were established in each of the four plant communities. Ten quadrats (20×20 cm each) were ran-

domly distributed in each plot to investigate the density and composition of the vegetative offspring coming from the belowground bud bank. Ramets along with their attached belowground plant parts (up to 20 cm depth) were sampled in each quadrat. The type of vegetative offspring was defined according to the type of the belowground bud bank as follows: (1) tiller-ramets, originated from buds located at the shoot base of bunchgrasses and rhizomatous grasses; (2) rhizome-ramets, originated from the rhizome nodes on rhizomatous grasses; (3) bulb-ramets, coming from buds located at the shoot base of bulbiform species; and (4) root-derived ramets, which grow out from the roots of some species (Fig. 2, Table 2).

After soil removal, samples were placed into plastic bags and transported to the laboratory for ramet identification and counting. Ramets originated from rhizomes and roots could easily be distinguished visually. However, stem bases of bunchgrasses and bulbs needed to be dissected for ramet counting. Dissection was conducted under a binocular microscope (×10). Only those ramets with chlorenchyma and photosynthetic tissues were considered in this study. The number of ramets per square meter (i.e., density) was first calculated from each 20×20 cm subplot. Thereafter, the average density was obtained

for each plot. Also, species composition was determined on each subplot; this information was used to determine the mean proportion of hemicryptophytes, geophytes and chamaephytes on each of the study plant communities along the grassland degradation gradient. Life forms were determined following R a u n - k i a e r (1934).

Statistical analysis

Prior to assessment, data was tested for normality (Kolmogorov-Smirnov test) and homoscedasticity (Fmax test), and it conforms to normal distribution law and homoscedasticity. One-way ANOVA was applied to analyze differences in the (1) total ramet densities, coming from all four study belowground bud banks, (2) proportion of ramets (coming from the different study bud banks) and

life forms, and (3) density within each ramet type, among the four study plant communities along the grassland degradation gradient. When F tests were significant at the level of $P<0.05$, means were compared using the LSD test (S t e e l and T o r r i e 1960). Significance tests were done with SPSS software package (SPSS 18.0).

RESULTS

Differences in total vegetative offspring density along the grassland degradation gradient

The average ramet density was significantly higher ($P <0.05$) in the *Stipa grandis + Leymus chinensis* plant community than in other plant communities (3484±290, Fig. 3). The lowest ($P <0.05$) ramet density occurred in
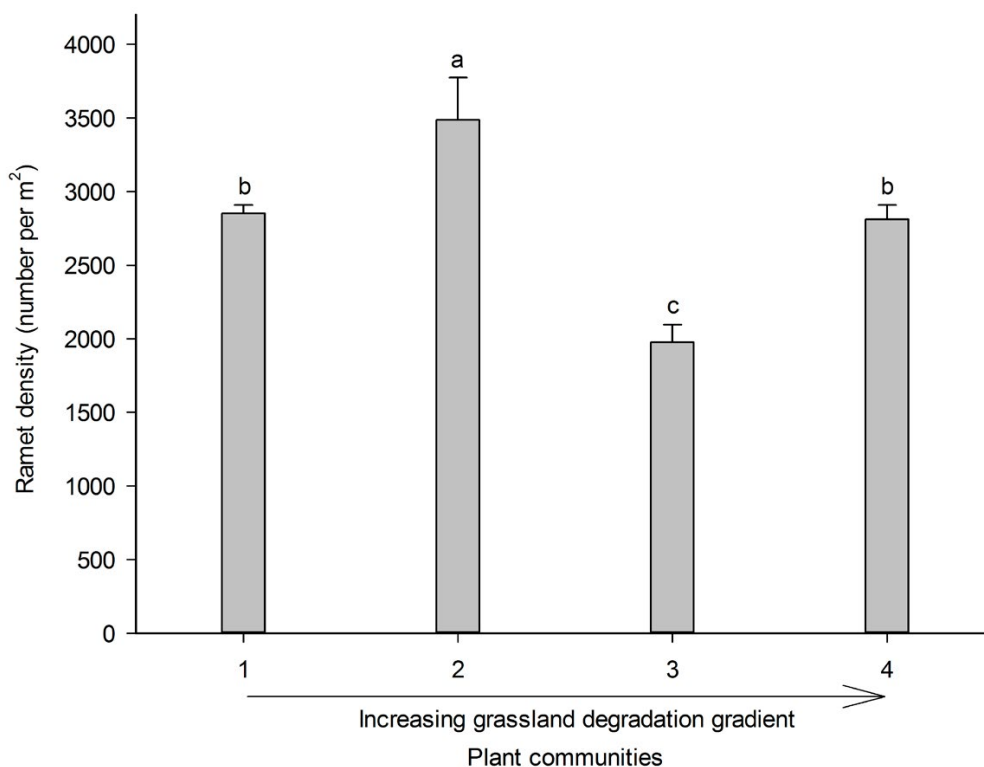

Fig. 3. Changes in the total vegetative ramet density coming from different bud banks (see Fig. 2) along the grassland degradation gradient on a typical steppe of Inner Mongolia (see Table 1). 1: *Leymus chinensis + Stipa grandis* + Perennial ruderals; 2: *Stipa grandis + Leymus chinensis* + Small bunch grasses; 3: *Artemisia frigida + Leymus chinensis* + Perennial ruderals; 4: *Potentilla acaulis + Leymus chinensis + Stipa grandis* + Perennial ruderals. The degree of grassland degradation in the X axis increases from 1 to 4 as indicated by the arrow. Values are means of n = 3. Vertical lines above histograms indicate one standard error of the mean. Different letters indicate significant differences ($P <0.05$) in total ramet density among plant communities.
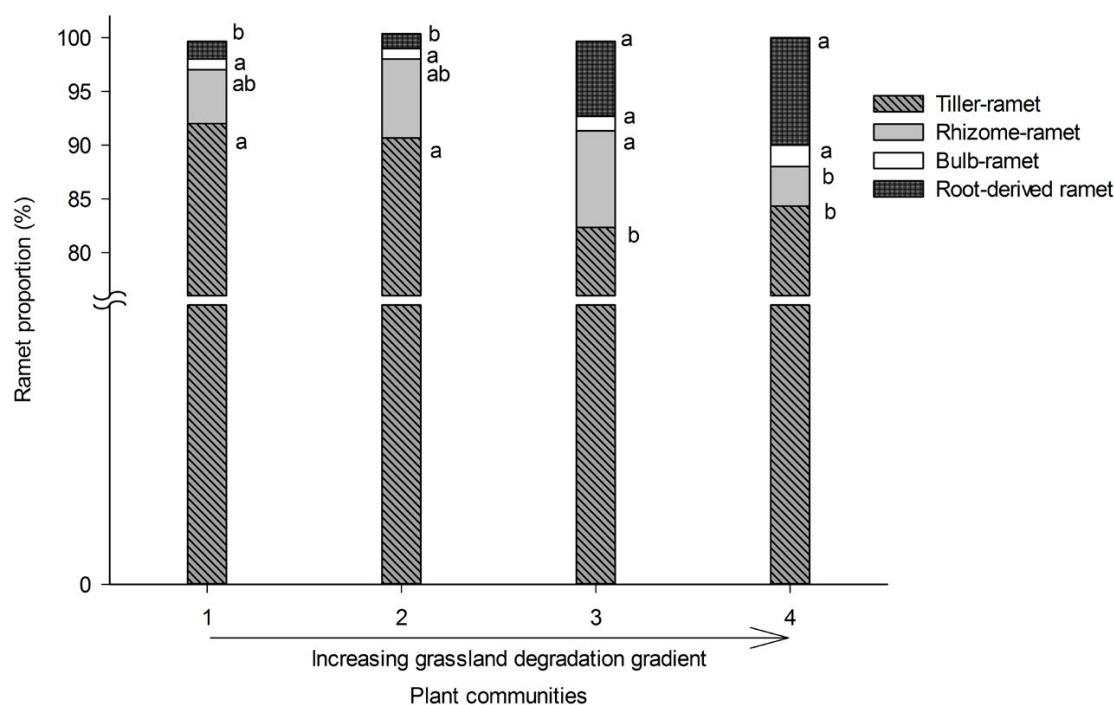
Fig. 4. Proportion (%) of vegetative ramet types coming from different bud banks (see Fig. 2) within each of the plant communities along the grassland degradation gradient on a typical steppe of Inner Mongolia. For explanations see Table 1 and Fig. 3. The degree of grassland degradation on the *x* axis increases from 1 to 4 as indicated by the arrow. Values are means of n=3. Different letters indicate significant differences (*P*<0.05) in the proportion of each ramet type among the four study plant communities.

the community dominated by *Artemisia frigida + Leymus chinensis* (1977±120, Fig. 3). No significant difference (*P*> 0.05) in total ramet density was showed between 1 and 4 communities (Fig. 3).

Vegetative offspring originated from different bud types along the grassland degradation gradient

Tiller-ramets accounted for the majority (82–92%) of the total ramet density in all four community types along the grassland degradation gradient (Fig. 4). However, the proportion of tiller-ramets was significantly greater (*P* <0.05) in the earlier (community types 1 and 2: *L. chinensis + S. grandis*, and *S. grandis + L. chinensis*) than later (community types 3 and 4: *A. frigida + L. chinensis*, and *P. acaulis + L. chinensis + S. grandis*) stages of grassland degradation (Fig. 4). At the same time, the trend of root-derived ramets showed an opposite pattern (*P* <0.05). The proportions of rhizome- and bulb-ramets did not differ sig-

nificantly (*P*> 0.05) among the whole study grassland degradation gradient (i.e., communities from 1 to 4, Fig. 4).

Contribution to recruitment from tillering (i.e., tiller-ramets) dominated that originating from any of the other belowground bud bank types in all four study communities (Fig. 5). The changes in the density of tiller-ramets followed the same trend with total ramet density changed along the grassland degradation gradient (Fig. 3 and 5). Rhizome-ramet density increased first (*P* <0.05) and then decreased significantly (*P*<0.05) along the grassland degradation gradient (Fig. 5). Root-derived ramet densities were significantly higher (*P*<0.05) in later (*A. frigida + L. chinensis*, and *P. acaulis + L. chinensis + S. grandis*) than earlier (*L. chinensis + S. grandis*, and *S. grandis + L. chinensis*) stages of the grassland degradation gradient (Fig. 5). Along this gradient, there were no significant changes (*P*> 0.05) in bulb-ramet densities (Fig. 5).

Relative contribution of life forms to total species richness along the grassland degradation gradient

The percentage contribution of hemicryptophtes to total plant species richness decreased (P <0.05, Fig. 6), while that of geophytes increased (P <0.05, Fig. 6) with increased levels of grassland degradation. The only chamaephyte species, *Artemisia frigida*, represented 15% of total species richness at intermediate levels of grassland degradation (i.e. community 3).

DISCUSSION

The whole contribution of belowground bud banks to population recruitment along the grassland degradation gradient

Total ramet recruitment from various belowground bud banks was greatest or lowest at intermediate stages of grassland degradation, or it reached medium values at low and high pressures of grazing and mowing. The vegetative offspring density in the *Stipa grandis* + *Leymus chinensis* plant community (the second stage within the grassland degradation gradient) was significantly higher than those in other plant communities, while that of the third stage within the gradient (*Artemisia frigida* + *L. chinensis*) was the lowest (Fig. 3). Despite the *L. chinensis* steppe is the most important pasture in northern China, inappropriate grazing is considered the key reason for its degradation (Tong *et al.* 2004). Our results showed, however, that high levels of grazing and mowing leaded to an increase of the belowground bud density and its sprouting ability, thus contributing to the replacement of tissues lost to herbivores. Other studies have reported that disturbances might stimulate vegetation regeneration by favoring species with the ability to re-sprout from belowground buds (Klimešová and Klimeš 2003). In particular, the high capacity of grassland ecosystems to respond rapidly to disturbance might be linked to their capacity of fast re-growth, mainly from bud banks (Knapp and Smith 2001, Clarke *et al.* 2013). On the other hand, when levels of grazing and/or mowing have been inappro-

priate (i.e., severe), they have showed a negative effect on plant recruitment from belowground bud banks (Busso *et al.* 1989, 2003), thereafter leading to grassland deterioration. This might partially be attributed to the decrease in the aboveground resource supply needed for belowground bud maintenance and outgrowth (Busso *et al.* 1989).

The existence of the dominant sub-shrub species *A. frigida* at intermediate levels of the grassland degradation gradient reduced the community regeneration via the belowground bud bank (Fig. 2). It has been reported that shrub encroachment reduces the abundance of hemicryptophytes (i.e., of stem bases producing tiller-ramets) (Busso 1997). This agrees with our results showing the lowest proportion of ramets derived from tiller buds in the presence of *A. frigida* in the community 3 (Fig.4).

Total ramet densities were similar at the lowest and highest levels of grassland deterioration within the study gradient of grassland degradation (Fig. 3). The increased densities of root-derived ramets (Fig. 4 and 5) and the presence of *Potentilla acaulis* at the greatest study levels of grassland degradation (i.e., community 4, Table 1) may have contributed to this finding. *P. acaulis* is well adapted to heavy grazing (Li 2009).

The relative regenerative contribution of different bud types along the grassland degradation gradient

Our results indicate that the specific bud type differently contributed to the aboveground plant community formation (Fig. 4 and 5). Buds may differ in resource storage and ability to grow out into vegetative regenerative tissues due to their different energy investment (Vesk and Westoby 2004), thus potentially contributing differently to population regeneration. The contribution of tiller buds to total ramet density was significantly higher during early than later stages of vegetation degradation (Fig. 4). However, they accounted for the majority of the total vegetative offspring density (more than 80%) independently of the stage of vegetation degradation in the study gradient (Fig. 4). This is partially because of the inherent greater tiller

(i.e., ramet) production from each parent bud in hemicryptohytes than in any other of the study life forms (i.e. geophytes: see Table 2). Some hemicryptophytes might produce up to 12 buds per parent tiller (e.g., *Agropyron desertorum*: Mueller and Richards 1986) at its stem base, and allow outgrowth of up to 3 of them when environmental conditions are appropriate during the growing season (Mueller and Richards 1986). Even more, new daughter tillers might grow out from buds located at the sheath bases at the same time than their single parent tiller is growing in some hemicryptophytes (e.g., *Nassella clarazii*, syn.: *Stipa clarazii*, Becker *et al.* 1997). Total precipitation during the period October 2011 to May 2012 was 93.9 mm. During the same period, the long-term average precipitation (1981–2010) was 59.2±5.1 mm. Thus, higher precipitation levels during this period than the long-term average value could help

to explain the greatest contribution from tiller buds (i.e., hemicryptophytes) than that from geophytes (Table 2) to total ramet density throughout the whole degradation gradient. It is well known that higher soil moisture levels contribute to determine a higher regrowth from tillers buds in hemicryptophytes e.g., *Agropyron desertorum* and *A. spicatum* (Busso *et al.* 1989) or *Stipa gynerioides* (Flemmer *et al.* 2003). At the same time, the higher monthly average air temperature during May 2012 (14.7°C) than the long-term average value (1981–2010; 13.5±0.2°C) might have contributed to a greater re-growth from the axillary buds of hemicrypthophytes. The positive effect of higher temperatures on the development of lateral buds has been well established on hemicryptophyte plant species e.g., *Lolium* spp (Mitchell 1953) or *Lolium perenne* (Hunt and Thomas 1985). Our results indicate that buds which grew out into
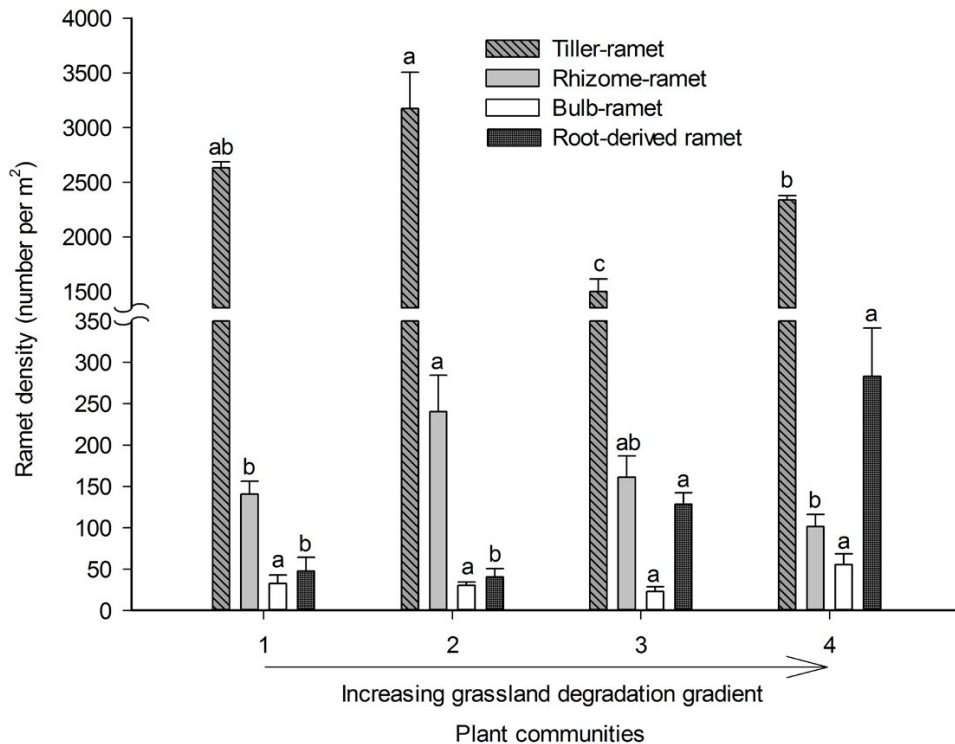

Fig. 5. Density of different vegetative ramet types in various plant communities along the grassland degradation gradient on a typical steppe of Inner Mongolia (see Table 1 and Fig. 3 for explanations). The degree of grassland degradation increases from 1 to 4 as indicated by the arrow. Values are means of n=3. Vertical lines above histograms indicate one standard error of the mean. Different letters indicate significant differences ($P < 0.05$ in ramet density within each ramet type in all four study plant communities.
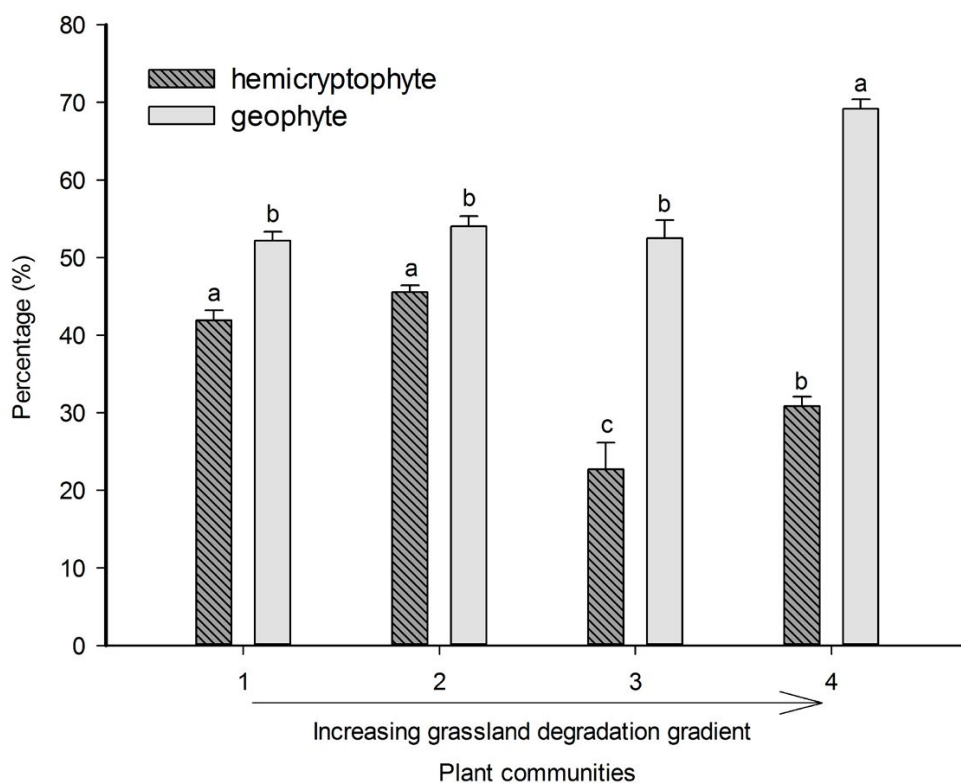
Fig. 6. Change in the proportion of hemicryptophytes and geophytes along the increasing grassland degradation gradient on a typical steppe of Inner Mongolia (see Table 1 and Fig. 3 for explanations). The degree of grassland degradation increases from 1 to 4 as indicated by the arrow. Values are means of n = 3. Vertical lines above histograms indicate one standard error of the mean. Different letters indicate significant differences ($P < 0.05$) in the proportional change of each life form (i.e., hemicrypthophyte or geophyte) along the increasing grassland degradation gradient.

tillers play the most important role in population regeneration and community composition throughout the whole grassland degradation gradient. This was in spite of species having tiller buds seemed to contribute relatively more to total ramet density during the early stages of vegetation degradation.

The relative contribution of tiller buds (i.e., tillering) to total ramet density decreased when grassland degradation increased. Greater levels of grazing pressure might have determined a reduced tiller production on the hemicryptophyte species. Several studies have reported a reduced tiller production under increasing defoliation pressures in several hemicryptophytes (e.g., *Agropyron desertorum* and *A. spicatum*: Busso *et al.* 1989, Briske and Richards 1995). Also a fewer number of axillary buds per tiller has been reported under high levels

of defoliation either under or not the exposure to water stress conditions (Busso *et al.* 1989, Humphreys 2005).

Under relatively light grazing, within the increasing study grassland degradation gradient, resource allocation might be either maintained or increased to rhizomes from aboveground plant parts. This might help to explain that the regenerative contribution of rhizome buds first increased and then decreased with the increases of vegetation degradation within the study gradient. Various defoliation tolerant or sensitive species have maintained resource allocation to belowground organs immediately after defoliation (Briske and Richards 1995, Dawson *et al.* 2000). However, it appears that resource allocation to rhizomes might be reduced under increasing stages of grassland deg-

radation. Thus, there might not be enough resources that can be used for the formation and maintenance of rhizome bud bank. Under this scenario, rhizomatous grasses would be replaced by other plant groups, and subsequently grassland degradation will increase. This might contribute to explain the decrease in rhizome-ramets under increasing levels of grassland degradation (Fig. 4).

Both the percentage and density of bulb-ramets did not change significantly along the grassland degradation gradient. It shows that (1) the regenerative contribution of bulb buds to total ramet density was relatively stable, and (2) species possessing bulb buds (e.g., *Allium anisopodium*) seem to be an essential component in the community composition along the study grassland degradation gradient.

Contrary to results on tiller-ramets, the percentages and densities of root-derived ramets were greater on later than earlier stages of the grassland degradation gradient. This indicates that with increases in grassland degradation, species with root-derived buds (e.g., *Potentilla acaulis*) will tend to increase in plant communities.

Relative contribution of life forms to total species richness along the grassland degradation gradient

The relative contribution of hemicryptophyte plant species to total species richness decreased while that of geophytes increased when comparing the two most extreme study levels of grassland degradation (i.e. communities 1 and 4, Fig. 6). It is well known that the growth apex (during early developmental stages) and axillary buds are at or slightly under the soil surface in hemicryptophytes (Raunkiaer 1934). In geophytes, on the other hand, vegetative stage renewal buds are deeper in the soil than those of hemicryptophytes. It might be that active renewal tissues (i.e., growth apex, crown buds) of tillers (i.e., ramets) could be pulled-off from the soil by grazing sheep much easier than active renewal tissues (i.e., buried-buds) on geophytes. Previous studies have shown that tillers can be pulled off from the soil by grazing livestock, which contributes to a reduction in the soil bud bank of hemicryptophytes (Tal-

lowin 1985, Bahmani *et al.* 2001). Alonso (1997) studied the effects of various grazing levels on the range of life forms in four grassland communities of Northern Spain. He reported that hemicryptophytes were the most abundant life form in all communities, and they increased their number under ungrazed conditions. In our study, the density of tiller-ramets coming from stem bases (hemicryptophytes) were more than 80% of total ramet density along the whole study gradient of grassland degradation.

There were changes in the relative contribution from the different bud types to total vegetative regeneration as the grassland degradation increased: while tiller buds played a relatively more important role in population regeneration during earlier than later stages of grassland degradation, plant species with root-derived buds were relatively more important in later than earlier grassland degradation stages on the *Leymus chinensis* steppe of Inner Mongolia. Also, throughout the increase in the grassland degradation process, population regeneration from rhizome buds first increased and then decreased, while that of bulb buds remained stable. Finally, the relative contribution of hemicryptophyte plant species to total species richness decreased, while that of geophytes increased at the extreme study levels of grassland degradation. Therefore, as grassland degradation increased, changes in the proportion of tiller-, rhizome- and root-derived ramets with respect to total ramet density determined in turn changes in the proportion of hemicryptophytes and geophytes in the study plant communities.

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