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Contribution of different bud types to community regeneration on a typical steppe under various enclosure durations in Inner Mongolia, China

Contribución de diferentes tipos de yemas a la regeneración de una comunidad en una estepa típica expuesta a varios tiempos de clausura en los pastizales del interior de Mongolia, China

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Abstract. Understanding the changes in the total bud bank, and its contribution to community regeneration, in response to grassland enclosure to livestock grazing, is crucial for grassland management. Despite its importance, the contribution of the total bud bank and that of different bud types to community regeneration as a whole have been rarely explored. The vegetative offspring recruited from different bud types was investigated in grasslands having different enclosure durations to livestock grazing on a typical steppe of Inner Mongolia, China. Total vegetative offspring density was significantly higher ($p<0.05$) under continuous grazing than in fenced grasslands, but no significant changes were found among plots with different enclosure durations to livestock grazing. The percentage and density of tiller-ramets were significantly higher ($p<0.05$) under continuous grazing than in fenced grasslands. However, rhizome-ramets followed an opposite pattern ($p<0.05$). Bulb-ramets showed negligible differences in percentage and density among grasslands with different enclosure durations to livestock grazing and those exposed to continuous grazing. Root-derived ramets only occurred in fenced plots. Our results indicate that (1) grassland enclosure to domestic livestock reduce vegetative regeneration from belowground bud banks; (2) enclosure duration to livestock grazing showed no evident effect on the whole contribution of the belowground bud bank to vegetative regeneration, but changed the relative contribution of the different bud types, and (3) while grassland enclosure to livestock grazing reduced density of tiller-ramets, rhizome- and root-derived sapling densities were increased. Therefore, changes in the regenerative contribution of different bud types might be used to (1) predict community dynamic under disturbances and climatic changes, and (2) delineate adequate policies for grassland management and utilization

Keywords: Grazing; Bud banks; Vegetative regeneration; Reproduction ecology; Restoration ecology.

Resumen. El entendimiento de los cambios en el banco de yemas total, y su contribución a la regeneración de la comunidad, bajo condiciones de clausura al pastoreo es crucial para el manejo de los pastizales naturales. A pesar de su importancia, la contribución del banco de yemas total, y el de los diferentes tipos de yemas a la regeneración de la comunidad vegetal raramente se ha explorado. La descendencia vegetativa obtenida de diferentes tipos de yemas se investigó en pastizales que diferían en el tiempo de su clausura al pastoreo en una estepa típica del interior de Mongolia, China. La densidad total de la descendencia vegetativa fue significativamente mayor ($p<0,05$) bajo pastoreo continuo que en las clausuras, pero no se observaron cambios significativos entre parcelas con diferentes tiempos de clausura al pastoreo. El porcentaje y densidad de las macollas hijas fueron significativamente mayores ($p<0,05$) bajo pastoreo continuo que bajo condiciones de clausura. Sin embargo, las macollas provenientes de rizomas mostraron un modelo opuesto ($p<0,05$). El porcentaje y densidad de juveniles provenientes de bulbos mostraron diferencias muy pequeñas entre pastoreo continuo versus parcelas con diferentes tiempos de clausura el pastoreo. Los juveniles provenientes de raíces se hallaron solo en las parcelas clausuradas al pastoreo. Nuestros resultados indicaron que (1) las parcelas clausuradas al pastoreo reducen la regeneración vegetativa desde los bancos de yemas subterráneos; (2) la duración del tiempo de clausura al pastoreo no mostró un efecto evidente respecto a la contribución total del banco de yemas subterráneo, pero cambió la contribución relativa de los diferentes tipos de yemas, y (3) la densidad de macollas hijas se incrementó, y la de juveniles provenientes de rizomas y bulbos se redujo, con la exclusión de las especies al pastoreo. Por lo tanto, los cambios en la contribución de diferentes tipos de yemas a la regeneración se podrían usar para (1) predecir la dinámica de la comunidad bajo disturbios y cambios climáticos, y (2) obtener medidas adecuadas para el buen manejo y utilización de los pastizales naturales.

Palabras clave: Pastoreo; Bancos de yemas; Regeneración vegetativa; Ecología reproductiva; Ecología de la restauración.

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INTRODUCTION

Grassland degradation caused by overgrazing and other inappropriate land uses have been recognized as a major threat to ecosystem services and functioning worldwide, especially in arid and semi-arid ecosystems (Mainguet, 1994; Bai et al., 2007; Ford et al., 2012; Wiesmeier et al., 2012). Disturbances affect population regeneration, or change population recruitment on plant functional groups with various reproduction modes (Latzel et al., 2011; Zhao et al., 2013). For example, changes in sexual reproduction as a result of disturbances (i.e., soil seed bank, seed germination and seedling establishment) have been explored extensively (Dreber & Esler, 2011; Mayer & Erschbamer, 2011; Cui et al., 2013). In contrast, the contribution of vegetative reproduction to population recruitment has rarely been explored (Klimesova & Klimes, 2007; Deng et al., 2010). In some herbaceous communities, the belowground reserve of meristems [the "bud bank" *sensu* Harper (1977)] plays a fundamental role in local population regeneration. For instance, while the soil seed bank played a negligible role in community regeneration in the tallgrass prairies of North America, more than 99% of aboveground shoots were recruited from the belowground bud bank (Benson et al., 2004; Benson & Hartnett, 2006). The bud bank is also of importance in population regeneration when grasslands are subjected to various disturbances (e.g., fire; grazing; nitrogen addition; mowing; drought; and artificial, simulated summer warming: Benson et al., 2004; Wang et al., 2004; Dalgleish et al., 2008; Dalgleish & Hartnett, 2009; Wang et al., 2010; Carter et al., 2012; Benot et al., 2013).

It is estimated that in the European flora, clonal growth organs can be categorized into 17 types according to their morphological characteristics (Kleyer et al., 2008; Klimesova & Bello, 2009). Accordingly, there may be various bud types in a given ecosystem (Klimesova & Klimes, 2007). Different bud types might respond differently to disturbances, and contribute differently to population regeneration (Klimesova & Klimes, 2007; Zhang et al., 2009). Adventitious buds on roots (e.g., *Euphorbia* spp. and biennials in general) may function like stem-base buds after an injury (Klimesova & Martinkova, 2004). Deeply-buried rhizome buds have contributed more to population recruitment after flooding than other bud types (Combroux & Bornette, 2004). Deeply-buried roots with adventitious buds can be used for population regeneration after severe disturbances (Malikova et al., 2012). In fire-prone habitats, many species cope with fire disturbance by root re-sprouting (Bell & Ojeda, 1999). Furthermore, different bud types could have different responses to different disturbance intensities, times and frequencies (e.g., Busso et al., 1989). With increasing severity, the effect of disturbance on plants and their buds can extend from above- to belowground (Frank, 2007). Therefore, belowground bud banks are assumed to be more resistant to severe disturbances than buds located aboveground. Besides, bud banks with different outgrowth timing could endow plants to cope with disturbances occurring at different times (Klimesova & Klimes, 2007).

Grazing, through biomass-removal and trampling can affect plant community assemblage by facilitating or suppressing some reproductive processes (e.g., bud banks). On a semi-arid savanna, bud density of the late-seral perennial grass *Bouteloua curtipendula* was 20% lower in a long-term grazing plot than in a fenced grassland. At the same time, bud density of the mid-seral perennial grass *Hilaria belangeri* was 190% higher in a long-term grazing plot than in fenced plots (Hendrickson & Briske, 1997). For different bud types, we assume that proper grazing might facilitate tiller buds by reducing shading of the stem bases in long-term grazed plots in comparison to long-term fenced grasslands (Briske & Richards, 1995). At the same time, rhizome buds would be comparatively suppressed because of a grazing-induced reduction of aboveground biomass production, and a subsequent carbon allocation belowground. Klimesova & Martinkova (2004) reported that adventitious buds on deep roots are probably very resistant to heavy grazing due to their profound position in the soil.

Grassland enclosure has been recognized as one of the most effective ways to preserve natural grasslands, and restore degraded ones (Yan et al., 2009). In recent years, changes in biotic and abiotic factors after grassland enclosure have been a focus of restoration ecology (Osem et al., 2004; Su et al., 2005; Jing et al., 2013). As a fundamental aspect in exploring the vegetation dynamics under grazing, plant regeneration has attracted an increasing attention in the past decades (Morgan, 2001; Kalamees & Zobel, 2002). However, in contrast to sexual reproduction, much less attention has been paid to asexual regeneration. Few studies have been published dealing with the dynamics and regenerative contribution of bud banks (Zhang et al., 2009). Compared with grazing, grassland enclosures might reverse community succession and exert contrasting effects on plants and their bud banks (Chaneton & Lavado, 1996; Meissner & Facelli, 1999; Su et al., 2005; Enright & Miller, 2007). However, the effect of grassland enclosures to livestock grazing on the (1) spatio-temporal pattern of bud banks; (2) response of different bud bank types, and (3) regenerative contribution of different bud types to community assemblage remain fully unexplored.

The typical steppe, with a surface area of about 4.1×10^5 km^2, as a part of the Eurasian Steppe (Han et al., 2009), accounts for about 10.5% of the temperate natural grasslands in China (Chen & Wang, 2000, Kang et al., 2007). The major plant community is constituted by *Leymus chinensis* + *Stipa grandis* (Yao et al., 2010). Grazing is the traditional land use on this grassland. Due to overgrazing and other inappropriate land uses, grassland degradation has become a severe problem in this region (Tong et al., 2004). As a result, plant communities currently include *Stipa grandis* + *Cleistogenes squarrosa*, *Ar-*

temisia frigida + *Stipa grandis* + *Leymus chinensis*, and *Potentilla acaulis* + *Stipa grandis* + *Cleistogenes squarrosa.* The dominant plant species are *Stipa grandis*, *Artemisia frigida* and *Potentilla acaulis* (Wu et al., 2011). Several measures have been taken by the central and local governments, and scientists have conducted many studies to preserve and restore this typical steppe (Tong et al., 2004; Han et al., 2009; Yao et al., 2010). However, studies on the effects of grassland enclosures to livestock grazing on different bud bank types, and their relative contribution to community regeneration, are lacking to date.

According to our previous field observations, plant population regeneration at the beginning of the growing season on the investigated steppe is mainly accomplished through the sprouting of the belowground, overwintering bud bank. Therefore, in the present study, we focused on the regenerative contribution of belowground, overwintering bud banks at the beginning of growing season. This was because of with the increase of air and soil temperatures, and the arrival of effective rainfall, the belowground, overwintering bud banks would most likely grow out and contribute to population regeneration at the start of growing season. In this study, we investigated the vegetative offspring originated from different bud types on grasslands with different enclosure durations on a typical steppe of Inner Mongolia, China. Our purposes were to answer: (1) how much each bud bank type does contributes to population recruitment when grasslands are subjected to different enclosure durations, and (2) what is the difference in the regenerative contribution between different bud types after grasslands have been enclosed for different periods. This study is helpful for predicting the community dynamics after various grassland enclosures, and implementing an effective management for the restoration of degraded grasslands.

MATERIALS AND METHODS

Study sites. This study was carried out at the Inner Mongolia Grassland Ecosystem Research Station (IMGERS, 43° 38' N, 116° 42' E, 1270 m.a.s.l.), Chinese Academy of Sciences. This station is well known for its long-term grazing, and nitrogen addition and grassland enclosure experimental plots (Bai et al., 2004; Fanselow et al., 2011; Schönbach et al., 2011; Giese et al., 2013). The climate is semi-arid continental. 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 temperatures range from -21.4 °C in January to 19.0 °C in July (1982–2008). Typically, maximum precipitation coincides with the highest temperature in June, July, and August (Schönbach et al., 2011).

In this region, grasslands are dominated by the perennial rhizomatous grass *Leymus chinensis*, and the perennial bunchgrass *Stipa grandis* (Yao et al., 2010). Overgrazing leads to different degrees of grassland degradation (Tong et al., 2004). As a result, some measures (e.g., grazing exclusion) were taken to preserve the natural grasslands, and restore those degraded. There are currently several experimental plots with different enclosure durations. In this study, four sites with different enclosure durations (i.e., treatments) were selected: (1) 33 years (enclosed since 1979), (2) 13 years (enclosed since 1999), (3) 7 years (enclosed since 2005), and (4) continuous grazing (CG; long-term stocking rate≈1.2 sheep units/ha). Plant communities fenced during 33 and 13 years were dominated by the perennial, rhizomatous grass *Leymus chinensis*, and the perennial bunchgrass *Stipa grandis*. Accompanying grass species included *Achnatherum sibiricum*, *Agropyron cristatum* and some perennial forbs, such as *Iris tenuifolia* and *Carex duriuscula*. *Stipa grandis* dominated the plant community fenced during 7 years; *Leymus chinensis* and some perennial bunchgrasses (e.g., *Cleistogenes squarrosa*) were companion species. Vegetation in the continuous grazing plots was dominated by *Stipa grandis*, although there was a large proportion of the perennial bunchgrass *Cleistogenes squarrosa*.

Sampling procedures. This investigation was conducted at the beginning of growing season (late-May) in 2012. Three plots, (100 m×100 m each), were established at each of four sites which had different enclosure durations (i.e., 33-, 22- or 7-year-old, or continuous grazing). Ten quadrats (20 cm×20 cm each) were randomly located in each plot to investigate the vegetative offspring composition of the study plant community: type, richness and abundance. The vegetative offspring along with their attached belowground parts (up to 20 cm depth) were sampled at each quadrat. The type of vegetative offspring was determined according to its morphological characteristics. Four types of ramets were found: (1) tiller-ramets, (2) rhizome-ramets, (3) bulb-ramets, and (4) root-derived ramets. Tiller-ramets originate from buds located at the stem base of bunchgrass and rhizomatous grasses. Rhizome-ramets originate from rhizome nodes. Bulb-ramets originate buds located at the shoot base of bulbiform species (e.g., *Allium bidentaum* and *A. tenuissimum*). Root-derived ramets sprout from the roots of some species.

Soil was carefully removed from the samples that were placed into plastic bags, and transported to the laboratory for ramet counting. Ramets from rhizomes and roots were easily distinguished visually, but stem bases of bunchgrasses and bulb-species needed to be dissected to identify tiller- and bulb-ramets. Only those ramets with chlorenchyma and photosynthetic tissues were considered in this study.

Statistical analysis. Before we analyzed the total ramet density and densities of different ramet types in plots with different durations of being enclosed, we transformed the original data set into the number of ramets per square meters and calculated the average for each plot.

One-way ANOVA was applied to analyze the differences in the total ramet density and densities of different ramet types in plots with different durations of being enclosed. LSD was used to compare the difference between different treatments. Significance tests were done with SPSS software package.

RESULTS

Total vegetative offspring density. Total vegetative offspring density was significantly higher ($p<0.05$) under continuous grazing than on fenced plots (Fig. 1). Plot enclosures of different durations showed a similar ($p>0.05$) total vegetative offspring density (Fig. 1).

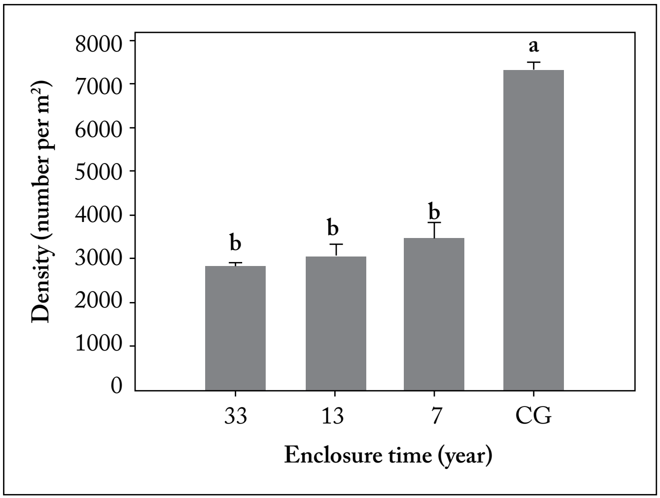

Fig. 1. Total density of vegetative offspring in grasslands with different enclosure durations. CG: continuous grazing. Each histogram is the mean of n=3. Different letters above histograms indicate significant differences at $p<0.05$.

Fig. 1. Densidad total de la descendencia vegetativa en pastizales naturales excluidos del pastoreo por diferentes períodos de tiempo (años). CG: pastoreo continuo. Cada histograma es el promedio de n=3. Letras diferentes sobre los histogramas indican diferencias significativas a $p<0,05$.

Vegetative offspring originated from different bud types. Tiller-ramets were from 91 to 99% of all ramets originated from the various bud types in the various enclosure durations (Fig. 2). Percentage and density of ramets were higher ($p<0.05$) when coming from stem bases, and lower ($p<0.05$) when originating from rhizomes, when comparing grazing versus fenced plots (Figs. 2 and 3). Except for the root-derived ramets in the CG treatment, ramets originated from buds at the stem bases, rhizomes, bulbs and roots in the remaining three treatments (Figs. 2 and 3). Density of rhizome-ramets were higher ($p<0.05$) in the 7- than in the 33-year-old and CG enclosures (Fig. 3).

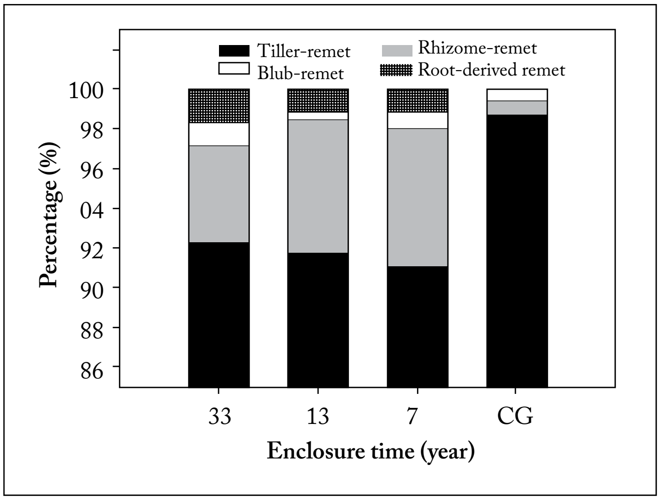

Fig. 2. Percentage of ramets originated from different bud types in grasslands exposed to different enclosure durations. CG: continuous grazing. Within each histogram, different shadings are the mean of n=3.

Fig. 2. Porcentaje de juveniles originados de tipos diferentes de yemas en pastizales naturales expuestos a períodos diferentes de exclusión al pastoreo. CG: pastoreo continuo. Dentro de cada histograma, sombreados diferentes son el promedio de n=3.

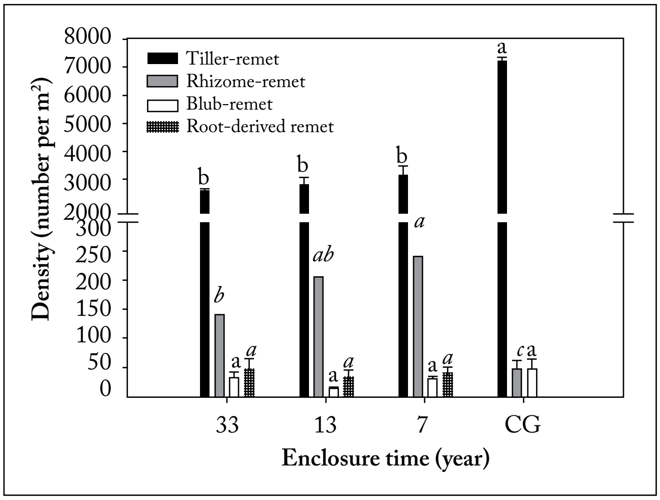

Fig. 3. Sapling densities originated from different bud types in grasslands exposed to different enclosure durations. CG: continuous grazing. Histograms are the mean of n=3. Different letters above histograms indicate significant differences ($p<0.05$) among the density of ramets originated from the same bud type in the different treatments.

Fig. 3. Densidad de juveniles originados de tipos diferentes de yemas en pastizales naturales expuestos a períodos diferentes de exclusión al pastoreo. CG: pastoreo continuo. Los histogramas son el promedio de n=3. Letras diferentes sobre los histogramas indican diferencias significativas ($p<0,05$) en la densidad de juveniles originados del mismo tipo de yema en los diferentes tratamientos.

DISCUSSION

Contribution to vegetative reproduction from various belowground bud banks in a grassland with different enclosure durations. Our results indicate that continuous grazing can facilitate vegetative regeneration via the belowground bud bank in comparison to grazing exclusion. However, the duration of grazing exclusion did not show differences in their vegetative offspring contribution from that bud bank. Increases in vegetative recruitment because of grazing in tallgrass prairie have been attributed to compensatory growth in response to grazing (Vinton & Hartnett, 1992). The mechanisms for the increase in vegetative offspring under grazing may be different for grasses and forbs. Such increases in grasses have been attributed to the grazing-induced bud dormancy release (Dalgleish & Hartnett, 2009). At the same time, those increases in forbs have been attributed to the increased belowground bud densities under grazing (Damhoureyeh & Hartnett, 1997). In any case, grazing leads to an increased vegetative offspring in both grasses and forbs (Dalgleish & Hartnett, 2009).

Grassland enclosures determine exclusion of grazing, and they might lead to suppressing effects on vegetative regeneration. This is because they can suppress the contribution of bud banks to community regeneration as a result of the negative effects of enclosures on bud bank sizes. In addition, grassland enclosures might lead to changes in the relative contribution of the different bud bank types to total vegetative regeneration. Liston et al. (2003) reported that grassland enclosures may change the relationship between sexual and vegetative reproduction, which might contribute to explain the decrease of the vegetative offspring in the fenced grasslands. The relationship between sexual and vegetative reproduction depends mainly on the resource allocation pattern of plants under different conditions (Reekie & Bazzaz 1987; Reekie & Avila-Sakar, 2005). When plants allocate relatively more resources into sexual reproduction, it is inevitable that they will allocate less resources into clonal growth (Obeso, 2002). Also, grassland enclosures might lead to increases of litter production, and soil nutrient and moisture contents, creating a more favorable environment for sexual reproduction (e.g., seed production; Bauer et al., 1987; Naeth et al., 1991; O'connor & Pickett 1992; Su et al., 2005). Finally, Winkler & Stocklin (2002) reported that a mixed strategy of clonal growth and reproduction by seeds was necessary to maintain populations of *Hieracium pilosella* L. in the presence of high interspecific competition and a shortage of open space in a calcareous grassland in NW Switzerland.

In the present study, we did not find significant differences in total ramet densities among enclosures that were excluded from grazing during various time periods. Results indicated that after a 7-year-enclosure from grazing, the contribution of total bud banks to community regeneration was relatively stable. Additional studies should test whether this pattern can be found in other grassland types.

Regenerative contribution from different bud types under various grassland enclosures to grazing. Our results supported the assumption that different types of buds contributed differently to population regeneration after exposure to (1) exclusion from grazing during various time periods or (2) continuous grazing. Grazing facilitated vegetative regeneration via tiller buds, while grassland enclosures facilitated vegetative regeneration via rhizome buds in the study community. This might be the result that the formation and reproduction of different bud bank types have different resource demands (Vesk & Westoby, 2004; Klimesova & Klimes, 2007). Compared with tiller production, the maintenance of a rhizome system and the production of rhizome-ramets need relatively more resources (Granéli et al., 1992; Asaeda et al., 2006). This suggests that resource availability might be greater on fenced than on grazing-exposed grasslands. This might allow fenced grasslands to meet the resource requirements for rhizome maintenance and rhizome-ramet production. On the other hand, tiller buds would have comparatively lower resource requirements which would be more easily satisfied under continuous grazing.

The fact that bulb-ramets occurred in all plots and did not change in percentage and density with enclosed duration suggests that they are relatively tolerant to grazing and grassland enclosure. Therefore, species with bulb buds appear to be essential components of community assemblage to buffer any negative effect due to disturbances. In contrast, root-derived ramets occurred only in fenced grasslands suggesting their lack of tolerance to continuous grazing.

Among the four types of ramets, only rhizome-ramets increased with decreasing enclosure duration (from 33 to 7 years). This indicates that long-term enclosure might affect the magnitude of the rhizome bud bank, and its contribution to community regeneration in this typical steppe. However, additional research should test why different bud types have different responses to enclosure duration and different contributions to vegetative regeneration.

Implications for grassland management and utilization. Understanding the dynamics of bud banks and their contribution to community regeneration in response to different grassland enclosures is essential for implementing an effective grassland management. Since grazing exclusion has a suppressing effect on vegetative regeneration from the bud bank when ramets come from rhizomes, appropriate grazing is necessary for community regeneration in the grassland. Our findings indicate that to restore *Leymus chinensis*-dominated pastures, short-term rather than long-term enclosures are needed. Vegetative regeneration from bulb buds was relatively stable in response to the four study treatments, indicating that species with bulb buds are tolerant to disturbance. Thereafter, we should consider making a better use of this plant functional group for grassland preservation and utilization.

CONCLUSIONS

Our study demonstrated that grassland enclosures to livestock grazing suppressed the vegetative regeneration via the total belowground bud bank in comparison to continuous grazing. Enclosure duration showed no obvious effects on the regenerative contribution from the total bud bank. However, it changed the relative contribution of different bud types to the vegetative regeneration. Tiller-ramets were reduced under enclosures to grazing while rhizome- and root-derived ramets were facilitated, and bulb buds kept constant in all treatments. Therefore, changes in the regenerative contribution of different bud types might be used to (1) predict community dynamic under disturbances and climatic changes, and (2) delineate adequate policies for grassland management and utilization.

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