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The disturbance and disturbance intensity of small and semi-fossorial herbivores alter the belowground bud density of graminoids in alpine meadows

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ABSTRACT

Do semi-fossorial herbivores influence the trajectory of plant community succession by altering belowground bud density in alpine meadows? Field surveys were carried out to investigate the effect of disturbance and disturbance intensity of the plateau pika (*Ochotona curzoniae*) on the belowground bud density in alpine meadows at two sites. The Linear Mixed Model (LMM) test and Linear Model (LM) test were used to analyze the relative effect of plateau pika disturbance on bud density and to clarify the response of belowground bud density to disturbance intensity. Our results showed that disturbance by the plateau pika increased belowground bud density of graminoids and plants from the grass and sedge families, including *Kobresia pygmaea* and *Elymus nutans*, but had no effect on forbs bud density. The bud density of graminoids, grass and sedge plants, and *K. pygmaea* and *E. nutans* showed a downward parabolic trend in response to increased disturbance intensity of the plateau pika, implying that there was an optimal level of disturbance intensity that maximized belowground bud density of graminoids. These results suggest that disturbance by the plateau pika has different effects on belowground bud densities of graminoids versus forbs. Additionally, disturbance by plateau pika up to the optimal intensity may improve grazing quality of alpine meadow in the long term through increasing graminoid bud density, resulting in a higher proportion of graminoids in pasture, while higher levels of disturbance by plateau pika may deteriorate alpine meadows through a reduction in graminoid bud density.

1. Introduction

The belowground bud bank has been shown to be an important indicator of the self-renewing ability of a plant community, and reflects the potential trend of grassland succession (Hendrickson and Briske, 1997; Hartnett et al., 2006; Ott and Hartnett, 2014). Many studies have shown that the seed bank contributes little to plant population recruitment (Rogers and Hartnett, 2001; Benson and Hartnett, 2006), and belowground reproductive modules and structures usually survive longer than aboveground shoots in a perennial grassland (Carter et al., 2012). Belowground buds are the main component of belowground reproductive modules and structure (Benson et al., 2004), and they grow new ramet via vegetative reproduction or develop new aboveground organ of plants via vegetative growth (Ott and Hartnett, 2015). Therefore, belowground buds are the main means by which perennial plants reproduce (López et al., 2001; Klimešová and Klimeš, 2007) and maintain their population in a perennial grassland ecosystem (Benson et al., 2004). Benson and Hartnett (2006) have even reported that more than 99% of aboveground shoots recruit from belowground buds in the tallgrass prairies. Plant communities require diversity in the size (density) and structure (age structure or spatial structure) of the belowground bud bank to regenerate plant populations with a large of proportion of perennial plants in a given community (Qian et al., 2014). The belowground bud bank is affected by biotic and abiotic factors (Dalgleish and Hartnett, 2008; Russell et al., 2015), and these factors, in turn, affect the self-renewing ability of the plant community. Many previous studies have focused on the effects of abiotic factors on the belowground bud bank and have found that the size and structure of the belowground bud bank are regulated by fire, mowing, soil moisture and nutrition, and light supply (Kroons and Hutchings, 1995; Dalgleish and Hartnett, 2008; Rusch et al., 2010; Carter et al., 2012; Clarke et al., 2013; Yu et al., 2017). Other studies have considered the effect of large grazing herbivores on the belowground bud bank and have shown that bison or cattle grazing alter the size and structure of the belowground bud bank in a grassland ecosystem (VanderWeide and Hartnett, 2015). In addition to large herbivores, small herbivores often live in colonies

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ranging from tens to thousands of individuals, and collectively create an extensive disturbance on grasslands by their burrowing behavior, consuming plant matter, or both (Davidson et al., 2012; Wu and Wang, 2017). However, whether small and semi-fossorial herbivores affect the belowground bud bank as much as do large grazing herbivores has not been well documented.

The plateau pika (*Ochotona curzoniae*), a common, social, semi-fossorial herbivore, affects alpine meadow in the Qinghai-Tibet Plateau (Smith and Foggin, 1999; Lai and Smith, 2003; Sun et al., 2015). This small herbivore directly affects alpine meadows by consuming plants, constructing burrow networks, and producing bare land (Yi et al., 2016; Liu et al., 2017) and indirectly by changing the regional soil moisture and soil temperature in disturbed areas (Guo et al., 2012a; Pang and Guo, 2017; Yu et al., 2017). The impact of plateau pika disturbance on alpine meadows often results in varied outcomes: plateau pika disturbance improves grazing quality of alpine meadows with a high proportion of graminoids (Wang et al., 2014; Pang and Guo, 2017) or deteriorates alpine meadows with high proportion of weeds. This variation in outcomes may be ascribed to disturbance intensity of the plateau pika (Smith and Foggin, 1999). Low disturbance intensity often increases the alpine meadows' species richness (Wangdwei et al., 2013), proportion of grass biomass (Yi et al., 2016; Pang and Guo, 2017), soil moisture (Guo et al., 2012a) and soil nutrition concentration (Yu et al., 2017), whereas high disturbance intensity usually reduces plant species richness (Wangdwei et al., 2013), proportion of grass biomass (Guo et al., 2012a), soil moisture (Guo et al., 2012a) and concentration of soil nutrition (Yu et al., 2017). These results illustrate how different disturbance intensities of the plateau pika can change the characteristics of a given plant community in alpine meadows, and more research is needed to understand how different disturbance intensities will lead to varied outcomes.

The belowground bud bank of a given plant represents its potential population in the plant community (Dalgleish and Hartnett, 2006; Clarke et al., 2013; Klimešová et al., 2014). Thus, diversity in the size and structure of the belowground bud bank of a given plant community is deemed very important for the potential composition of that existing plant community (Rusch et al., 2010), because persistence of the belowground bud bank is crucial for surviving environmental disturbances. Generally, belowground buds include four types: tiller buds, rhizome buds, root-derived buds and bulb buds (Qian et al., 2014). The potential plant community driven by plateau pika disturbance depends on the density, composition and emergence of the four belowground bud types of the entire plant population. The impact of plateau pika disturbance on the characteristics of the belowground bud bank indicate the successional direction of the existing plant community, and herald the potential plant community to some extent. Therefore, understanding the effect of plateau pika disturbance and its intensity on characteristics of the belowground bud bank may help explain why plateau pika disturbances often lead to improvement or deterioration of alpine meadows in the Qinghai-Tibetan Plateau.

Belowground bud density represents the potential plant recruitment ability of the belowground bud bank (Klimešová and Klimeš, 2007; Li et al., 2012) and is an indicator of the potential regeneration of the plant community. Plant communities in alpine meadows consist of graminoids and forbs (Bowman et al., 1995), and a higher ratio of graminoids generally indicates the improvement of the alpine meadow (Pang and Guo, 2017). Thus, the relative density of graminoid and forb belowground buds can indicate the potential improvement or deterioration of alpine meadows under plateau pika disturbance. The present study aimed to assess whether the presence and intensity of disturbance by the plateau pika affected the belowground bud density within two study sites. Specifically, we hypothesized that: (1) plateau pika disturbance affects the belowground bud density as much as do large herbivores; (2) graminoids' and forbs' belowground bud density responds differently to the disturbance and disturbance intensity the plateau pika, (3) changes in belowground bud density may explain how plateau pika disturbance improves or deteriorates alpine meadows in the Qinghai-Tibetan Plateau. This study thus attempts to present an example of how small and semi-fossorial herbivore disturbance regulates the potential successional direction of alpine meadows: improvement or deterioration.

2. Materials and methods

2.1. Study area description

The study areas were in Maqu County and Luqu County in Gansu Province, China; these two counties are on the eastern edge of the Qinghai-Tibet Plateau. The climate of the study areas is a typical plateau continental climate, with cold and humid characteristics. The average annual temperature is 1–3 °C, while the temperature rises above 12 °C in summer and falls below −10 °C in winter. The annual mean precipitation is 400–800 mm, 80% of which falls in the short summer growing season during the period of June to September, and the annual evaporation is 1000–1500 mm. The alpine meadows are widely distributed in the study areas and play an important role in water conservation and maintaining ecological safety aspects of the Yellow River Basin (Feng et al., 2010). Meadows dominated by the perennial *Kobresia pygmaea* are the main alpine meadow type in Maqu County and Luqu County. The plateau pika (*Ochotona curzoniae*) is one of the main small and semi-fossorial herbivores inhabiting *K. pygmaea* alpine meadows, because the low height of the plant community increases the ability of the animals to detect predators. These small herbivores have important impacts on plant composition and productivity (Guo et al., 2012b; Sun et al., 2015).

2.2. Experimental design

The plateau pikas live in family groups and their density is lower at the beginning of summer when the population consists mostly of overwintered adults, and peaks in August after multiple litters have been weaned on-site (Qu et al., 2013). At that time plateau pika disturbance reaches its highest level, including disturbance to the belowground bud density. Plateau pikas prefer to consume twigs, stems, leaves and flowers of forbs and sometimes consume twigs of graminoids, and they does not consume the belowground component of plants (Jiang, 1985; Liu et al., 2008). Plateau pika disturbance has been verified to alter the composition of plant community by increasing aboveground graminoid biomass and decreasing forb biomass (Pang and Guo, 2017).

The field experiments were conducted in a winter-grazed alpine meadow (no grazing during the survey period) at Gaxiu in Luqu County (102°18′E, 34°20′N) and at the Azi station of Maqu County (101°53′E, 33°40′N) during early August of 2016. At each site, we chose disturbed areas where plateau pikas were present and burrow entrances were observed in the field, and undisturbed areas that accordingly were selected by the apparent absence of plateau pikas and burrow entrances. Disturbed areas and undisturbed areas were restricted to *K. pygmaea* meadow at the two sites. At each site, we selected 10 disturbed areas and 10 undisturbed areas and they were paired. There were no obvious topographical differences between paired survey locations of the disturbed areas and undisturbed areas at each site. One plot of 25 m × 25 m was placed in each disturbed and undisturbed area, and the distance between plots was approximately 0.5 km. In disturbed areas, we recorded the active burrow entrance number in each plot by the "plugging tunnels method" for at least 4 days (Sun et al., 2015; Pang and Guo, 2017; Yu et al., 2017), and these surveys were conducted in a relatively fixed time sequence at each plot, between 09:00 and 11:30, in relation to the frequency of activities of plateau pikas (Zhang et al., 2005; Zeng and Lu, 2009). Within disturbed areas, the survey showed that densities of active burrow entrances for 10 plots were 304, 384, 432, 512, 576, 752, 864, 928, 1040, and 1216 per ha at the Azi station of Maqu County, and were 144, 160, 192, 208, 288, 352, 480, 528, 576, and 720 per ha at Gaxiu in Luqu County.

2.3. Sampling

In each plot, we randomly selected 10 subplots (20 cm width × 20 cm length × 20 cm depth). If a subplot was placed on a burrow we reselected the subplot within 1 m of the burrowing. After selecting subplots, we firstly quantified soil moisture content using time domain reflectometry (TDR), and then sampled soil cores in these subplots at 20 cm depth, together with the aboveground standing litter. The links between the aboveground standing litter and the belowground plant parts were kept intact (Qian et al., 2014), which allowed us to identify the belowground buds by the standing litter. Soil was carefully removed from each soil core in the field, and soil samples were collected and placed in a sealed sampling bag. All plant samples were then immediately placed in sealable plastic bags. The plant samples and soil samples were stored at 4 °C until further processing in the laboratory. For plant samples, we rinsed remnant soil from the belowground plant matter within two weeks, examined belowground plant organs using a dissecting microscope, and trimmed roots to allow complete examination of the belowground structures. We assigned buds to species and types using bud morphology, phyllotaxy, morphology of the attached root system, and morphology of any remaining aboveground parts (Bowman et al., 1995; Carter et al., 2012; VanderWeide and Hartnett, 2015). In this study, we just identified the tiller buds and rhizome buds, and did not identify root-derived buds and bulb buds. The quantity of total buds and bud type of each species was recorded for each subplot. We divided all species for each subplot into graminoid groups and forb groups, and recorded the appearance of species in disturbed and undisturbed areas at the two study sites. The forb species recorded at both sites were *Anemone rivularis, Potentilla anserine, Potentilla fragarioides,* and *Leontopodium alpinum.* Additionally, Maqu County had the forb species *Ajania pallasiana, Euphrasia pectinate, Gentiana macrophylla, Oxytropis kansuensis,* and *Potentilla bifurca*, and Luqu County had *Anaphalis lacteal* and *Swertia bimaculata* (Table S1). Belowground bud density for each plot was calculated by estimating the average value of 10 subplots.

Previous studies show that bud density is related to the soil moisture and soil nitrogen concentration (Aarssen, 2008; Rusch et al., 2010), and we measured soil moisture and soil nitrogen concentration in our subplots to check the results. The soil samples were air-dried at room temperature and pulverized. The dried soil samples were sieved through a 2-mm wire mesh to remove large particles. Samples were analyzed for soil nutrient concentrations. Soil total nitrogen (TN) was measured via the Kjeldahl procedure (Foss Kjeltec 8400, FOSS, Denmark).

2.4. Statistical analyses

The data from each plot were checked for normal distribution using the Shapiro-Wilk test. If necessary, the data were base-10 log-transformed to pursue the assumption of normality and homogeneity of variances. To determine whether the disturbance of the plateau pika significantly altered the belowground bud density, we used two complementary analyses, a Linear Mixed Model (LMM) and a Wilcoxon-Mann-Whitney test. The LMM was used to analyze the relative effect of plateau pika disturbance on belowground bud density of graminoid, forb and overall plant species. For this, bud density of each species acted as a response variable for the model, and the disturbed/undisturbed (Dist.), and the site (Site) were transformed into dummy variables and were used as predictors together with their interaction. Specifically, the disturbances value was added to the model as a random factor, which was estimated by assigning it to each pair of observations. If belowground bud density of graminoids or forbs was significantly affected by disturbance of the plateau pika, we further selected main plant families in the graminoid group or the forb group to check whether the disturbance of the plateau pika significantly affected the belowground bud density of that plant family. If the belowground bud density of the selected plant family was affected by plateau pika disturbance, we chose the main species in the selected plant family to confirm whether plateau pika disturbance had affected the belowground bud density of that main species. If the disturbance of the plateau pika significantly influenced belowground bud density of the selected species, we checked the relationships between the number of each bud type of that species and plateau pika disturbance. In addition, to clarify the response of belowground bud density to disturbance intensity, the densities of active burrow entrances were considered as a fixed factor, and this was used to construct a regression analysis via a Linear Model (LM). To clarify the response of graminoid bud density to soil nitrogen concentration and soil moisture, the soil nitrogen concentration and soil moisture were considered as fixed factors, and these fixed factors was used to construct a regression analysis via a Linear Model (LM). To select the final regression models that indicated the effect of active burrow entrance densities, soil nitrogen concentration and soil moisture on belowground bud density, likelihood ratio tests were used to compare the simple linear regression and polynomial regression models.

The non-parametric Wilcoxon-Mann-Whitney tests were used to evaluate the effects of plateau pika disturbance on belowground bud density in each site, because soil cores from disturbed and undisturbed sites were paired and generally not normally distributed. This complemented the analysis with the LMM, as the non-parametric Wilcoxon-Mann-Whitney tests could identify the effects of plateau pika disturbance on belowground bud density that were specific to each site, which may have gone undetected in the LMM. All statistical analyses were performed with R Version 3.2.2.

3. Results

3.1. Effects of disturbance of plateau pika on bud density of graminoid and forb group, and the grass and sedge families

The disturbed/undisturbed of disturbance (Dist.) and the two study sites (Site) had significant effects on the forb bud density, while they had no significant effect on the total bud density and graminoid bud density (Table 1) or the grass bud density and sedge bud density (Table 2).

The study site significantly affected forb bud density, grass bud density and sedge bud density. The disturbance of the plateau pika significantly affected the total bud density, graminoid bud density, grass bud density and sedge bud density, but it had no effect on forb bud density. The total bud density, graminoid bud density, grass bud density and sedge bud density in disturbed areas were significantly higher than in the areas devoid of plateau pikas across the two study

Table 1
The density of forb bud, graminoid bud and total bud in relation to the disturbance by plateau pika (disturbances), in the alpine meadow of Maqu County and Luqu County, based on Linear Mixed Models.

Response variable	Linear mixed models (Dist. as a random factor)					
	Site		Dist.		Dist. × Site	
	F	p value	F	p value	F	p value
Total bud	0.107	0.746	**18.233**	**0.000**	0.112	0.740
Forb bud	**4.839**	**0.034**	4.397	0.051	8.132	**0.007**
Graminoid bud	0.114	0.737	**13.445**	**0.001**	0.279	0.601

Bud density of each group acts as a response variable while the predictors were: the disturbed/undisturbed of plateau pika (Dist.), the two study sites (Site), and the interaction of both. The factor of Dist., which account for the paired design, acted as a random variable. Significant p values (< 0.05) are in bold.

Table 2
The density of grass bud and sedge bud in relation to the disturbance by plateau pika (disturbances), in the two most disturbed sites of the alpine meadow in Maqu County and Luqu County, based on Linear Mixed Models.

Response variable	Linear mixed models (Dist. as a random factor)					
	Site		Dist.		Dist. × Site	
	F	p value	F	p value	F	p value
Grass bud	**80.444**	**0.000**	**29.450**	**0.000**	0.339	0.504
Sedge bud	**5.801**	**0.021**	**7.070**	**0.012**	0.198	0.659

Grass bud density and sedge bud density acts as a response variable while the predictors were: the disturbed/undisturbed of plateau pika (Dist.), the two study sites (Site), and the interaction of both. The factor of Dist., which account for the paired design, acted as a random variable. Significant p values (< 0.05) are in bold.

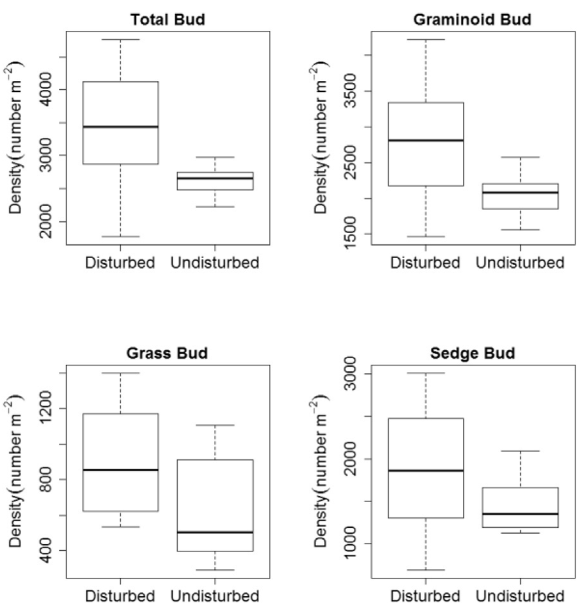

Fig. 1. Values of the density of total bud, graminoid bud, grass bud and sedge bud significantly differs between areas disturbed and undisturbed by plateau pika activities. The values were obtained from the Linear Mixed Models on the disturbance of plateau pika disturbances in the alpine meadow of Maqu County and Luqu County (Gansu Province, China).

sites (Fig. 1).

The two sites had different responses of forb bud density to the disturbance of the plateau pika. Forb bud density was significantly higher in disturbed areas than in undisturbed areas in Maqu County, while it was not significantly different between disturbed areas and undisturbed areas in Luqu County (Table S2). The grass bud density in disturbed areas was significantly higher than that in undisturbed areas in the two study sites (Table S3), while the sedge bud density was significantly higher in disturbed areas than in undisturbed areas in Luqu County and was not significantly different between disturbed areas and undisturbed areas in Maqu County.

3.2. Effects of the disturbance of the plateau pika on density of tiller buds and rhizome buds of K. pygmaea and E. nutans

The disturbed/undisturbed of plateau pika (Dist.) and the two study sites (Site) had significant effects on tiller bud density and rhizome bud density of *K. pygmaea*, while there were no effects on total bud density of *K. pygmaea* or total bud density, tiller bud density and rhizome bud density of *E. nutans* (Table 3).

The disturbance of the plateau pika significantly affected tiller bud density, rhizome bud density and total bud density of the two species, which were increased in the two study sites (Fig. 2). Similarly, the study site had significant effects on tiller bud density, rhizome bud density, total bud density of *E. nutans*, and tiller bud density of *K. pygmaea*.

Disturbance by the plateau pika increased total bud density and rhizome bud density of *K. pygmaea* and total bud density, tiller bud density and rhizome bud density of *E. nutans* in Maqu County (Table S4). It also increased tiller bud density and rhizome bud density of *K. pygmaea* and total bud density and tiller bud density of *E. nutans* in Luqu County, while there were no effects on total bud density of *K. pygmaea* or rhizome bud density of *E. nutans*.

3.3. Effects of disturbance intensity of the plateau pika on bud density of graminoids and forbs, and the grass and sedge families

Total bud density, forb bud density, graminoid bud density and sedge bud density showed a similar trend of increasing and then decreasing in response to the increase of disturbance intensity in Maqu County and Luqu County, whereas forb bud density showed no obvious trend (Figs. 3 and 4). Grass bud density showed an upward unimodal trend in Luqu County, but had no obvious trend in Maqu County (Fig. 4).

3.4. Effects of disturbance intensity of the plateau pika on tiller buds and rhizome bud densities of K. pygmaea and E. nutans

Total bud density, tiller bud density and rhizome bud density of *K. pygmaea* and *E. nutans* showed a downward parabolic trend with increased disturbance intensity across the two study sites (Figs. 5 and 6).

3.5. Relationship between graminoid bud density and soil total nitrogen concentration, soil moisture

Graminoid bud density increased as the soil nitrogen concentration and soil moisture increased in the study areas (Fig. 7).

4. Discussion

Our findings clearly demonstrate a strong link between the disturbance by the plateau pika and belowground bud density within different plant groups (forb group and graminoid group), plant families (grass family and sedge family), and plant species (*K. pygmaea* and *E. nutans*) in alpine meadows, and our results verify that small and semi-fossorial herbivores alter belowground bud density, as is known for large grazing herbivores. We find that the disturbance of the plateau pika increases the graminoid bud density in alpine meadows; however, large grazing herbivores decrease graminoid bud density in tallgrass prairie (Dalgleish and Hartnett, 2008; VanderWeide and Hartnett, 2015) and semiarid savanna (Hendrickson and Briske, 1997), and increase graminoid bud density in Brazilian Campos grasslands (Fidelis et al., 2014). These differences in response of graminoid bud density to herbivores are ascribed to dominant plants in grassland and disturbance patterns of herbivores. In tallgrass prairie, semiarid savanna and alpine meadows, rhizomatous grasses are dominant, while tussock grasses dominate in Brazilian Campos (Boldrini and Eggers, 1997). Plateau pikas disturb the alpine meadow by consuming twigs, young stems and leaves of forbs and some graminoids (Jiang, 1985; Liu et al., 2008) and constructing a burrow system (Bagchi et al., 2006; Sun et al., 2015), whereas the large grazing herbivores disturb the grassland by consuming all leaves and stems of graminoids and trampling. The consumption patterns of the plateau pika may eliminate apical dominance and cause the production of more axillary buds (Cline, 1997; Hendrickson and Briske, 1997), whereas the consumption of large grazing herbivores encourages rhizomatous graminoids to allocate more nutrients for compensatory growth of aboveground shoots (Belsky, 1992; Burns et al., 2009) and increase bud output in order to maintain the plant density (Qian et al., 2014), resulting in a reduction

Table 3
The density of total bud, tiller bud and rhizome bud of *Kobresia pygmaea* and *Elymus nutans* in relation to the disturbance by plateau pika (disturbances), in alpine meadow at Maqu County and Luqu County, based on Linear Mixed Models,

Response variable		Linear mixed models (Dist. as a random factor)					
		Site		Dist.		Dist. × Site	
		F	p value	F	p value	F	p value
Kobresia pygmaea	Total bud	3.895	0.056	**12.303**	**0.001**	1.528	0.224
	Rhizome bud	0.324	0.573	**9.513**	**0.004**	**6.590**	**0.015**
	Tiller bud	**12.381**	**0.001**	**5.732**	**0.022**	**3.658**	**0.004**
Elymus nutans	Total bud	**106.783**	**0.000**	**18.622**	**0.000**	0.475	0.495
	Rhizome bud	**36.710**	**0.000**	**4.499**	**0.041**	0.161	0.690
	Tiller bud	**73.763**	**0.000**	**22.886**	**0.000**	0.335	0.566

Total bud density, rhizome bud density and tiller bud density of *K. pygmaea* and *E. nutans* acts as a response variable while the predictors were: the disturbed/undisturbed of plateau pika (Dist.), the two study sites (Site), and the interaction of both. The factor of Dist., which account for the paired design, acted as a random variable. Significant p values (< 0.05) are in bold.

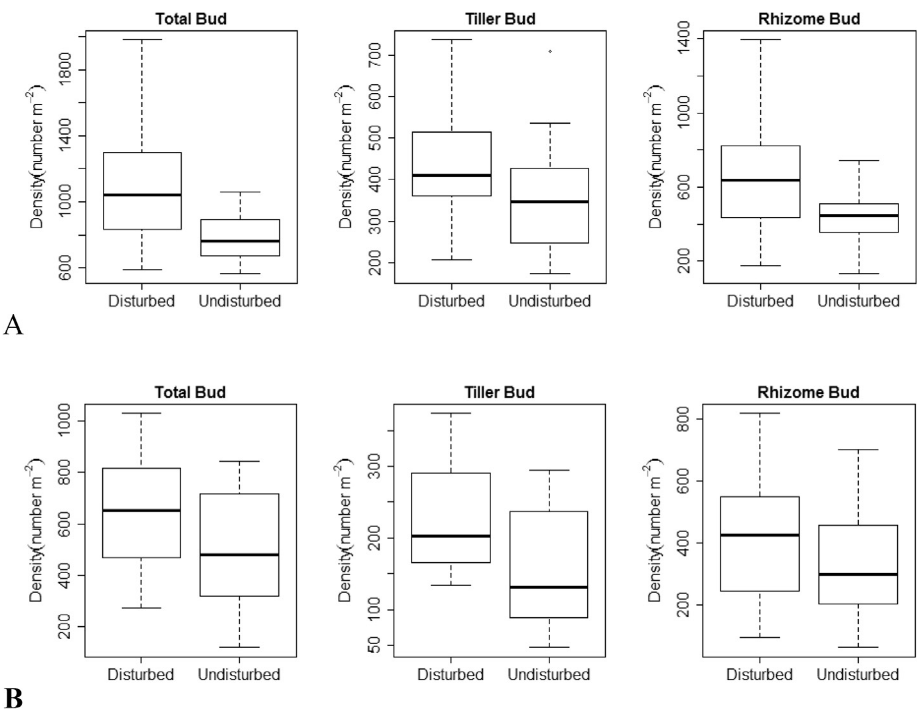

Fig. 2. Values of the density of total bud, tiller bud and rhizome bud of *Kobresia pygmaea* (A) and *Elymus nutans* (B) that significantly differs between areas disturbed and undisturbed by plateau pika activities. The values were obtained from the Linear Mixed Models on the disturbance of plateau pika disturbances in the alpine meadow of Maqu County and Luqu County (Gansu Province, China).

of nutrient supplies for the belowground buds or a reduction of the original bud density of rhizomatous graminoids. Disturbances by plateau pika increase soil nitrogen concentration and soil moisture in our study (Fig. S1, Table S5), and the graminoid bud density increases linearly with the increase of soil moisture and soil nitrogen concentration (Fig. 7). High soil moisture and soil nitrogen concentration in disturbed areas enable graminoids to produce more buds and this is also reported in the literature (Aarssen, 2008; Dalgleish et al., 2008; Rusch et al., 2010; Chen et al., 2015). Trampling by large herbivores often decreases soil moisture and nitrogen concentration (Rui et al., 2011), resulting in reduction of belowground buds of rhizomatous graminoids (Dalgleish et al., 2008; Mofidi et al., 2012; Chen et al., 2015), and stimulating tussock grasses to produce more tiller buds (Fidelis et al., 2014), resulting in an increase of graminoid bud density in Brazilian Campos grasslands. Our finding is also consistent with the effect of fire on belowground bud density. Fire releases the competition abilities of the subordinate grasses and forbs (Benson et al., 2004), and encourages graminoids with high recruitment to produce more buds.

There are two possible reasons for the lack of an effect of plateau pika disturbance on forb bud density: firstly, the plateau pikas prefer short-stem legumes when compared to graminoids, and so reduce bud density of legumes by consuming them (Jiang, 1985); secondly, the disturbances of the plateau pika provide good habitats for forbs? and those opportunistic species produce more buds. Thus, the tradeoff between annual opportunistic forbs and legumes leads to plateau pika disturbance having no overall effect on total forb bud density.

K. pygmaea and *E. nutans* are the main species in the sedge family and grass family in our alpine meadows (Bowman et al., 1995; VanderWeide and Hartnett, 2015; Yu et al., 2017) and their belowground buds consist of tiller buds and rhizome buds. Our results show that disturbance by the plateau pika increases grass bud density and sedge bud density, as well as *K. pygmaea* and *E. nutans* bud density, implying that disturbance by the plateau pika can lead to an increased proportion of *K. pygmaea* and *E. nutans* in plant community, resulting in improving grazing quality of alpine meadow in the long term. There are several possible reasons for this: firstly, *E. nutans*, a pioneer species, increases potential belowground bud density because it expands its spatial distribution via colonizing bare patches (Guo et al., 2012b), while the disturbance of the plateau pika encourages *K. pygmaea* to produce more buds in order to defend against intrusion of annual or dicotyledon opportunist (Hartnett et al., 2006). Secondly, the foraging of plateau pika often stimulates *K. pygmaea* and *E. nutans* to produce

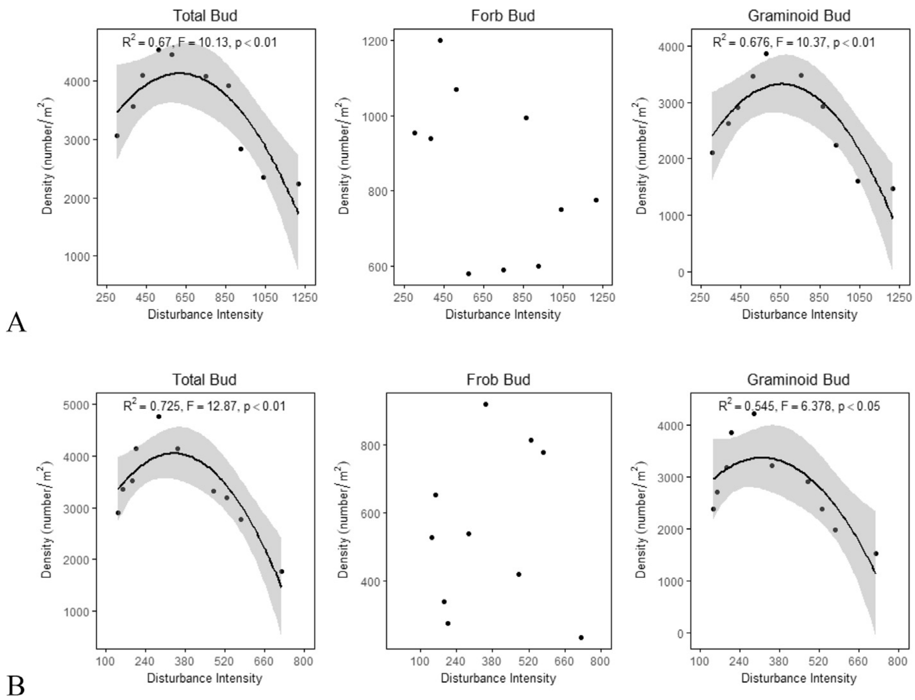

Fig. 3. The density of total bud, graminoid bud and forb bud for different disturbance intensity of plateau pika in Maqu (A) and Luqu (B) County was based on a Linear Model. For a detailed visualization of the relationship between disturbance intensity and bud density, an adjusted local smoothed regression line (black) is shown with its 95% confidence interval in gray. Disturbance intensity: active burrow entrances of plateau pika per plot.

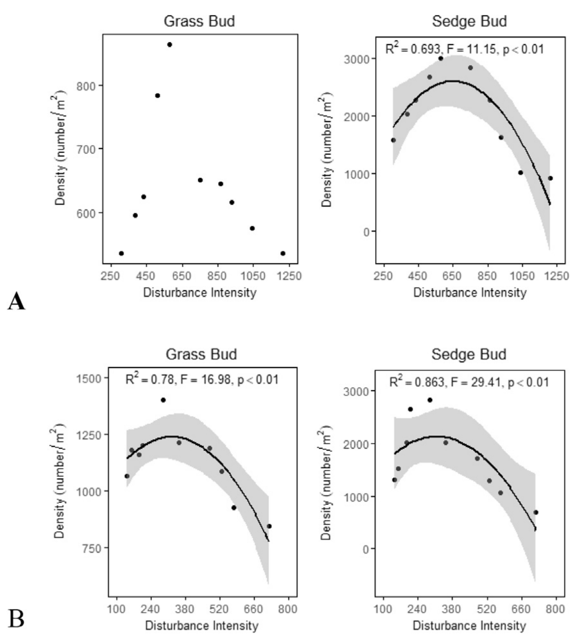

Fig. 4. The density of grass bud and sedge bud for different disturbance intensity of plateau pika in Maqu (A) and Luqu (B) County was based on Linear Model. For a detailed visualization of the relationship between disturbance intensity and bud density, an adjusted local smoothed regression line (black) is shown with its 95% confidence interval in gray. Disturbance intensity: active burrow entrances of plateau pika per plot.

more tiller buds for recruitment to the aboveground population (Jiang, 1985), and thirdly, the high soil nitrogen concentration and soil moisture created by plateau pika disturbance provide conditions beneficial for the development of *K. pygmaea* and *E. nutans* rhizome buds.

With the exception of forb bud density, total bud density and graminoid bud density had a downward parabolic trend in response to increased disturbance intensity of plateau pika. These results suggest that there is an optimal level of plateau pika disturbance that is conducive to maximizing the total bud density and graminoid bud density under ideal conditions. There are several reasons for this. Firstly, soil moisture and soil nitrogen concentration show downward parabolic trends in our study (Fig. S2), and this will contribute to downward trends of total bud density and graminoid bud density. Secondly, the increase of bare patches rapidly decreases the available living space for plants when disturbance intensity is above the optimum level (Bagchi et al., 2006), which leads plant density to decline, and further decreases bud density. Thirdly, plateau pika's consumption of plants up to the optimal disturbance level is less than that beyond the optimal disturbance level, which leads to alternative outcomes: low consumption is beneficial to removing bud apical dominance, resulting in more bud production, whereas high consumption damages the whole plant structure, decreasing the potential for bud production.

The rhizome bud density of *K. pygmaea* and *E. nutans* shows the downward parabolic trend, whereas tiller bud density of *K. pygmaea* and *E. nutans* shows no significant trend with the increase of disturbance intensity of plateau pika. The rhizome bud density is highly correlated with the soil nitrogen concentration (Pan et al., 2004; Aarssen, 2008; Rusch et al., 2010). These results suggest that the response of rhizome bud density of grasses and sedges to disturbance by the plateau pika may be thought of as a possible indicator of how plateau pika disturbances may improve or deteriorate grazing quality of alpine meadows.

5. Conclusions

The composition of the belowground bud bank is considered a good indicator of the potential plant community in a grassland ecosystem. We have verified in this study that small herbivores also have a significant effect on underground bud density; however, the effect of small herbivores on underground bud density showed different patterns to results from big herbivore disturbance. Our study shows that the disturbance of plateau pika increases graminoid bud density but has no effect on forb bud density. The effect of disturbance by plateau pika on underground bud density of selected? Plant families and species also support the results from the graminoid functional group. It seems likely that the different responses of underground bud density to disturbance by herbivores of different sizes are dependent on ways those herbivores cause disturbance to grasslands and the dominant species in the studied grasslands.

We also find that the positive or negative effects of the disturbance

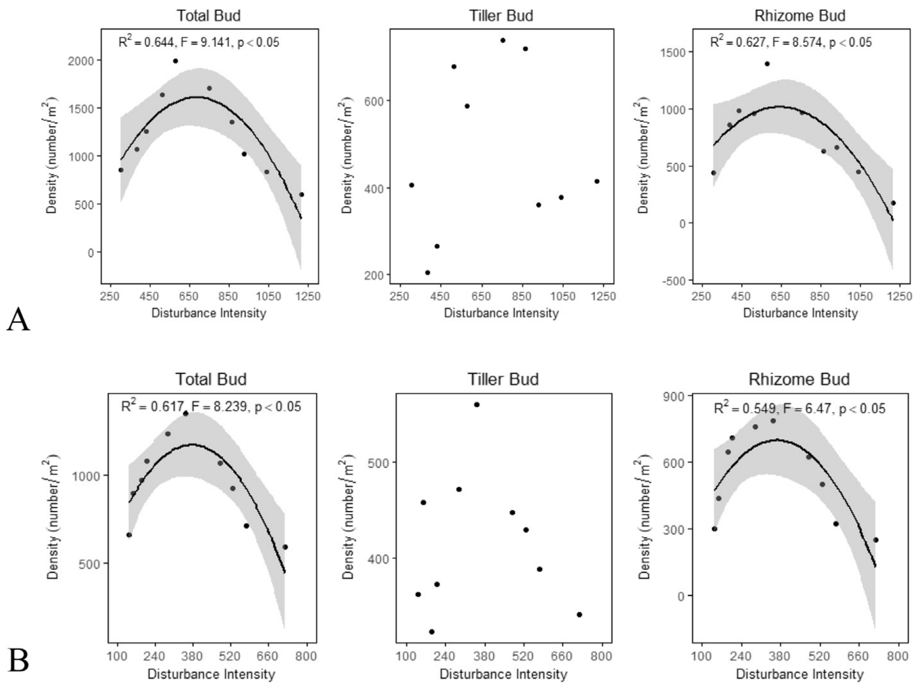

Fig. 5. The density of tiller bud, rhizome bud and total bud of *Kobresia pygmaea* for different disturbance intensity of plateau pika in Maqu (A) and Luqu (B) was based on Linear Model. For a detailed visualization of the relationship between disturbance intensity and bud density, an adjusted local smoothed regression line (black) is shown with its 95% confidence interval in gray. Disturbance intensity: active burrow entrances of plateau pika per plot.

of plateau pika on belowground bud density are dependent on disturbance intensity of plateau pika. Total bud density and graminoid bud density show upward parabolic trends in response to increased disturbance intensity of plateau pika, suggesting that there is an optimal level of disturbance intensity of plateau pika for belowground bud density. This disturbance level is conducive to maximizing the total bud density and graminoid bud density under ideal conditions. Distinctive composition of belowground bud density indicates that the potential plant community will vary with changes in disturbance intensities by plateau pika in the long term. Consequently, increased plateau pika disturbance up to this optimal level will improve grazing quality of alpine meadow due to higher graminoid bud density but supra-optimal levels of disturbance will deteriorate alpine meadow by decreasing graminoid bud density. Therefore, our study presents a possible hypothesis for how different disturbance intensity of small burrowing herbivores leads to improvement or deterioration of alpine meadows.

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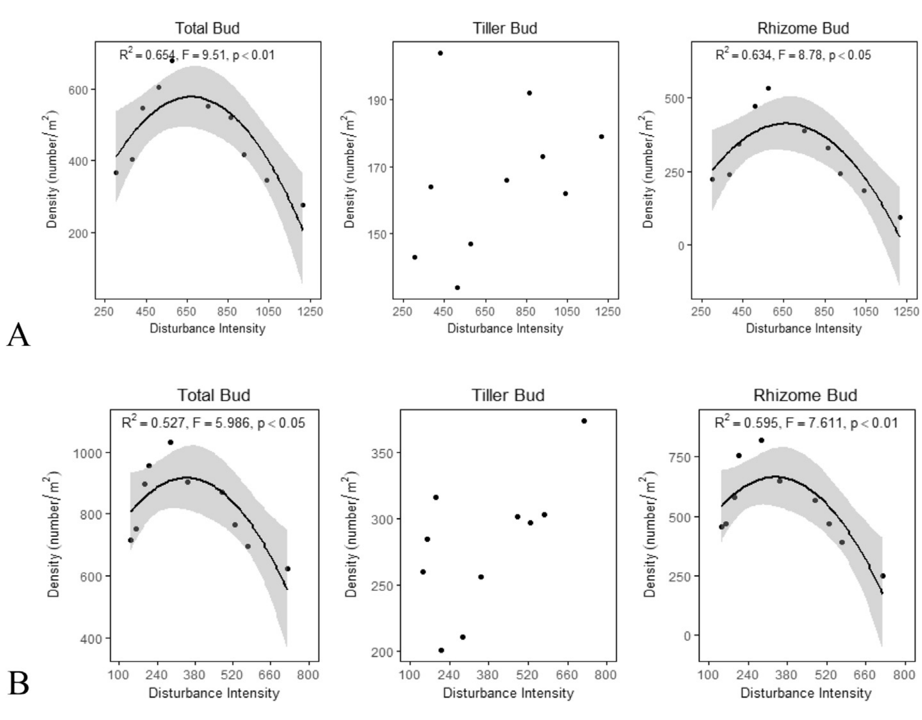

Fig. 6. The density of tiller bud, rhizome bud and total bud of *Elymus nutans* for different disturbance intensity of plateau pika in Maqu (A) and Luqu (B) was based on Linear Model. For a detailed visualization of the relationship between disturbance intensity and bud density, an adjusted local smoothed regression line (black) is shown with its 95% confidence interval in gray. Disturbance intensity: active burrow entrances of plateau pika per plot.

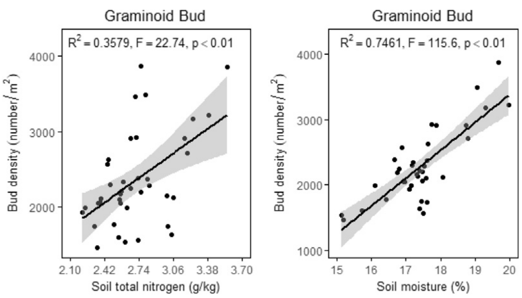

Fig. 7. The graminoid bud density in different soil total nitrogen and soil moisture on disturbance and undisturbance areas in Maqu County and Luqu County was based on Linear Model. For a detailed visualization of the relationship between soil total nitrogen, soil moisture and bud density, an adjusted local smoothed regression line (black) is shown with its 95% confidence interval in gray.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecoleng.2018.01.003.

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