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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