Geoderma 307 (2017) 98–106

Contents lists available at ScienceDirect

Geoderma

journal homepage: www.elsevier.com/locate/geoderma

Soil disturbance and disturbance intensity: Response of soil nutrient concentrations of alpine meadow to plateau pika bioturbation in the Qinghai-Tibetan Plateau, China

Cheng Yu, Jing Zhang, Xiao Pan Pang, Qian Wang, Yu Pei Zhou, Zheng Gang Guo*

State Key Laboratory of Grassland Agro-Ecosystems, College of Pastoral Agriculture Science and Technology, Lanzhou University, Lanzhou City 730020, PR China

ARTICLE INFO

Handling Editor: Yvan Capowiez

Keywords:
Plateau pika
Bioturbation
Disturbance
Kobresia pygmaea meadow
Soil nutrient

ABSTRACT

Plateau pikas (*Ochotona curzoniae*) bioturbation affects the soil nutrient concentrations of the alpine meadow in the Qinghai-Tibetan Plateau (QTP) by the arrangement of bare land. This study investigated the effect of the disturbance produced by plateau pika bioturbation on primary soil nutrient concentrations of the *Kobresia pygmaea* meadow in view of overall and site scale and further analyzed the effect of the disturbance intensity of plateau pika on the soil nutrient concentrations of vegetated land and bare land. Our results showed that the disturbance by plateau pika bioturbation significantly decreased the soil organic carbon (SOC), total nitrogen (TN) and total phosphorus (TP), and increased the available phosphorus (AP), NO_3^--N and NH_4^+-N of bare land. Moderate disturbance intensities increased the SOC, TN and TP of both vegetated land and bare land and reduced the NO_3^--N, NH_4^+-N and AP of vegetated land while increasing those of bare land. Disturbance within the threshold disturbance intensities of plateau pika is beneficial to the soil C and N, accumulating higher available nutrient concentrations in the topsoil, which would provide good habitats for certain rare plants and supply nutrients for the nitrophilous graminoid plants to grow well in the QTP. These results suggest that the understanding of the responses of the soil nutrient concentrations to plateau pika bioturbation should consider the bare land under disturbance intensities of plateau pika and alpine meadow type.

1. Introduction

Bioturbation is considered to be a major driver for dynamic variation of ecosystem function because it often alters a soil's physical and biotic processes (Reichmana and Seabloomb, 2002; James et al., 2009) and improves the soil health (James et al., 2009; Fleming et al., 2014). Most visible bioturbation is generally produced by small burrowing mammals (Reichmana and Seabloomb, 2002; James et al., 2009; Wilkinson et al., 2009), which usually manipulate the substrate soil and create a variety of disturbances via the arrangement of bare land produced by their direct burrowing activities (Schooley and Bestelmeyer, 2000; Fleming et al., 2014). This disturbance manifests itself as a discrete mosaic of vegetated land and bare land over a range of spatial scales (Yu et al., 2016; Pang and Guo, 2017; Yu et al., 2017), which induces differences in soil nutrient concentrations between bare land and vegetated land (James et al., 2009; Xu et al., 2012; Kurek et al., 2014). Previous studies have shown that small burrowing mammals often can rapidly alter the soil nutrient concentrations compared to other plant-driven and geomorphic processes (Villarreal et al., 2008; Fleming et al., 2014).

Plateau pika (*Ochotona curzoniae*) is a mainly small and common burrowing mammal in the Qinghai-Tibetan Plateau (QTP) of China (Guo et al., 2012; Yu et al., 2016), and it has been considered as a keystone species of the alpine meadow ecosystem because of its greatly influential role (Smith and Foggin, 1999; Lai and Smith, 2003). Plateau pikas often live in colonies ranging from tens to thousands of individuals, and collectively, they induce drastic changes of soil nutrient concentrations (Smith and Foggin, 1999; Sun et al., 2015a; Wu et al., 2015) because soil in the alpine ecosystems is remarkably sensitive to small burrowing mammals (Körner, 2003; García-González, 2008). The *Kobresia pygmaea* meadow, one of the larger alpine meadow types, sustains native livestock production and biodiversity and maintains water conservation and soil erosion control in the QTP (Qi et al., 2008; Wu et al., 2015). This meadow is also a good habitat for plateau pikas due to its relatively low height of vegetation, which increases the ability of plateau pika to detect predators (Wangdwei et al., 2013). Thus, the *K. pygmaea* meadow is a representative example of how the disturbance of plateau pika affects soil nutrient concentrations.

Disturbance produced by plateau pika bioturbation in the alpine meadow remains a controversial issue. A number of professionals

* Corresponding author.
E-mail address: guozhg@lzu.edu.cn (Z.G. Guo).

http://dx.doi.org/10.1016/j.geoderma.2017.07.041
Received 28 April 2017; Received in revised form 20 July 2017; Accepted 31 July 2017

consider that bare land is detrimental to the alpine meadow because it reduces the land cover and decreases plant productivity (Dong et al., 2013; Sun et al., 2015a) or even develops a “black-soil-type” degraded grassland (Qi et al., 2008; Dong et al., 2013). Conversely, others argue that bare land is beneficial to the alpine meadow because it increases the water infiltration (Wilson and Smith, 2015) and available nutrients and maintains soil biodiversity (Zhou et al., 2010; Wu et al., 2015; Zhang et al., 2016). In fact, the amount of bare land is correlated to the disturbance intensity of plateau pika (Sun et al., 2015b; Wu et al., 2015).

There are also several ongoing debates concerning the effects of the disturbance intensities of plateau pika on the soil nutrient concentrations of the alpine meadow. Several studies showed that the soil organic carbon (SOC), total nitrogen (TN), total phosphorus (TP), and NH_4^+-N decrease, while NO_3^--N increases with the increase of the disturbance intensity of plateau pika (Liu et al., 2013; Sun et al., 2015a). Another study argued that the SOC, TN and inorganic nitrogen (NO_3^--N and NH_4^+-N) show no obvious relationship with the disturbance intensities of plateau pika (Peng et al., 2015). However, those studies neglected the difference in soil nutrient concentrations between vegetated land and bare land. Although Guo et al. (2012) proposed that moderate disturbance by plateau pika increases the soil organic matter, TN, and TP concentrations both of vegetation land and bare land, that study ignored the difference of alpine meadow types under different disturbance intensities of plateau pika. Therefore, more research is warranted to test the difference in soil nutrient concentrations of bare land and vegetated land for the same alpine meadow type.

This study aimed to assess the effect of the disturbance caused by plateau pika and the disturbance intensity of plateau pika on the soil nutrient concentrations of vegetated land and bare land in the *K. pygmaea* meadow across three sites. Specifically, we hypothesized that (1) the soil nutrient concentrations between vegetated land and bare land are inconsistent, (2) different disturbance intensities of plateau pika have different influences on the soil nutrients of vegetated land and bare land, (3) the response of soil nutrients in three study sites to the disturbance and disturbance intensities of plateau pika is inconsistent, and (4) an appropriate disturbance intensity of plateau pika is beneficial to soil nutrients in the QTP. These findings will provide more comprehensive information for understanding the influence of the plateau pika bioturbation on the soil nutrients.

2. Materials and methods

2.1. Study area description

The study sites were located in Luqu County (102°18′37″ E, 34°20′36″ N), Maqu County (101°53′15″ E, 33°40′41″ N) and Gonghe County (99°35′46″ E, 36°44′34″ N), which are situated in the QTP, China (Fig. 1). The altitudes of the study sites are 3550 m in Luqu County, 3530 m in Maqu County and 3750 m in Gonghe County. The study areas experience a cold and humid plateau continental climate with mean annual temperature of 1 °C to 3 °C and mean annual precipitation ranging from 600 mm to 800 mm in Luqu County and Maqu County and from 250 mm to 500 mm in Gonghe County, and 80% of the annual rainfall falls in the short summer growing season during the period of June–September. The mean annual potential evaporation is 1100 mm to 1300 mm in Luqu County and Maqu County and 800 mm to 1000 mm in Gonghe County.

The *K. pygmaea* meadow is the main and widest distribution alpine meadow in the three Counties where plateau pikas are present. The field survey was restricted to *K. pygmaea* meadow. The dominant species of this alpine meadow is *K. pygmaea*, which is a perennial forb and a native species, and its height is approximately 1–3 cm. The main associated plant species are *Elymus nutans*, *Poa pratensis*, *Anemone obtusiloba*, *A. rivularis*, *Potentilla anserine*, *P. fragarioides*, and *Saussurea hieracioides* (Yu et al., 2016; Pang and Guo, 2017; Yu et al., 2017). Based on the Chinese soil classification system (Gong, 2001), the soil type in the field survey areas is subalpine meadow soil with a mattic epipedon at approximately 7 cm in the topsoil, which is an organic matter-rich soil horizon. This alpine meadow is often grazed by yaks and Tibetan sheep via warm and cold season pastures rotational grazing. Overgrazing and high disturbance intensity of plateau pika are considered to contribute to the increase in soil erosion (Delibes-Mateos et al., 2011; Sun et al., 2015a) and lead to the alpine meadow degradation (Wangdwei et al., 2013).

2.2. Experimental design

The density of plateau pika population can grow rapidly within a relatively short period, with a peak in early August (Smith and Gao, 1991). During this period, plateau pika disturb the alpine meadow most (Guo et al., 2012). During the period of August 2015, the field surveys at the three sites were carried out in the winter-grazed alpine meadow (no grazing in growth season). Bare lands caused by plateau pika were easily visible and differed from the signs of disturbance caused by other animals. It was difficult to estimate directly the density of plateau pika population because the plateau pika is a social animal that moves and produces 2–5 litters (litter size range = 2–7) with a 3-week interval between each litter in the breeding season. Therefore, the density of active burrow entrances was used to indicate the disturbance intensity of plateau pika in the QTP (Guo et al., 2012; Sun et al., 2015b; Wu et al., 2015; Liu et al., 2017; Yu et al., 2017), similar to the *Spalacopus cyanus* in North-Central Chile (Escobedo et al., 2017).

At each site, 10 plots 25 m × 25 m in size were selected in the areas where plateau pikas were present. We plugged burrows for three days and recorded the number of plugs that were cleared by plateau pikas to allow access to the meadow surface (Guo et al., 2012; Desoky, 2015; Escobedo et al., 2017). The average number of burrow entrances per plot with plugs that were cleared by plateau pikas in three days was considered to be the value of active burrow entrances of that plot.

The bare land produced by plateau pika was always found near burrow entrances and showed a mosaic distribution in vegetated land. During the period of August 2015, five bare lands were randomly selected in each plot as bare subplots to collect the soil, and five vegetated subplots in vegetated land were determined by the corresponding position of bare subplots in order to ensure that the distance between vegetated subplot and bare subplot was approximately 1 m (Fig. 2). Before collecting soil samples, plant litter from the soil surface in subplots was cleared out. Next, 20-cm long soil cores were collected by a cylindrical metal core sampler 5 cm in diameter because most plant roots were within 10 cm of the soil surface (Bueno et al., 2013; Chen et al., 2017), and generally, the plateau pikas burrows did not go deeper than 20 cm (Wei et al., 2007). Five soil subsamples in each bare subplot were disaggregated and thoroughly mixed to provide a homogeneous and composite sample that was representative of the bare subplot, and four soil subsamples in each vegetated subplot were determined by the corresponding position of bare subplots (Fig. 2). We collected a total of 300 composite soil samples, of which 150 composite soil samples each were from bare subplots and vegetated subplot. The composite soil samples were stored in a cool box until further processing in the laboratory. The geographical coordinates of field survey sites at each county were recorded by using a handheld GPS (Garmin eTrex 201X, Garmin, USA).

2.3. Soil analyses

Each composite soil sample was air-dried at room temperature and pulverized. The dried soil samples were sieved through a 2-mm wire mesh to remove large particles (stones and gravel), loose vegetative debris and visible roots as much as possible and were used to analyze the soil nutrient concentrations. TN and SOC were measured via the Kjeldahl procedure (Foss Kjeltec 8400, FOSS, DK) and Walkley-Black

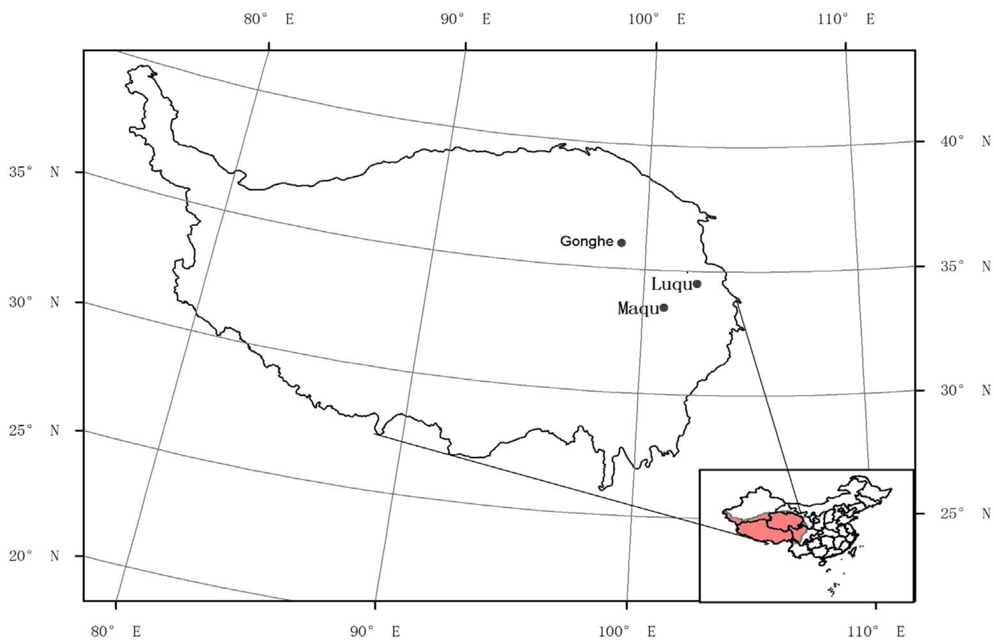

Fig. 1. Location of study sites in the Qinghai-Tibetan Plateau (QTP) of China. Mapped expansion of points Luqu County, Maqu County and Gonghe County correspond to three study sites, respectively.

method (Nelson and Sommers, 1982), respectively. TP and total potassium (TK) were measured by Mo-Sb colorimetry (UV-2102C, UNICO, Shanghai, China) and flame photometry (Model 2655-00 Digital Flame Analyzer, Cole-Parmer Instrument Company, Chicago, IL, USA), respectively, after the soil was digested with perchloric and nitric acid (Nelson and Sommers, 1982). Available nitrogen (nitrate nitrogen and ammonium nitrogen) was extracted with potassium chloride (KCl, 2 mol L^{-1}), and the concentrations were measured by the flow injection method (FIAstar 5000 Analyzer, FOSS, DK). Available potassium (AK) was extracted by NH_4OAc and was later measured by flame photometry (Nelson and Sommers, 1982). Available phosphorus (AP) was extracted by $NaHCO_3$ and was measured by Mo-Sb colorimetry (Nelson and Sommers, 1982).

2.4. Statistical analyses

For repeated-measure ANOVA (mixed-model ANOVAs), we used the *lme4* package in R for fitting linear mixed model (LMM) (Bates, 2005; Kabacoff, 2011). To determine whether the disturbance caused by plateau pika bioturbation significantly altered the soil nutrients, we used two complementary analyses, an LMM and a Wilcoxon-Mann-Whitney test. The LMM was used to analyze the relative effect of the disturbance on the soil nutrients at the three study sites, in which each soil nutrient acted as a response variable for the model, and the bare/vegetated subplots (Disturbance), as well as the three sites (Site) (that were transformed into dummy variables), and their interactions were introduced as predictors. Specifically, the Site was added to the model as a random factor, and the number of active burrows at each sample point as a covariate. In addition, we clarified the responses of soil nutrients to the disturbance intensity of plateau pika. The active burrow entrance densities were considered to be the fixed factor and these was used to construct a regression analysis. The regression curves of soil nutrients/disturbance intensity were obtained using the LOESS model or linear model (LM).

To evaluate the effects of the disturbance on the soil nutrients within each site, non-parametric Wilcoxon-Mann-Whitney tests were used because the soil samples were paired, and their normality could not be assumed (Moore et al., 2008; Bueno et al., 2013). These analyses complemented the LMM because they can identify the effects of the disturbance on the soil nutrients that were specific to each site, which might be undetected in LMM. All of the statistical analyses were performed with R Version 3.2.2.

3. Results

3.1. Densities of active burrow entrance in the three study sites

The field survey results showed that active burrow entrances of the 10 plots within disturbed areas were 144, 192, 288, 352, 416, 496, 576, 736, 832, and 896 per ha in Luqu County, 112, 192, 272, 384, 432, 512,

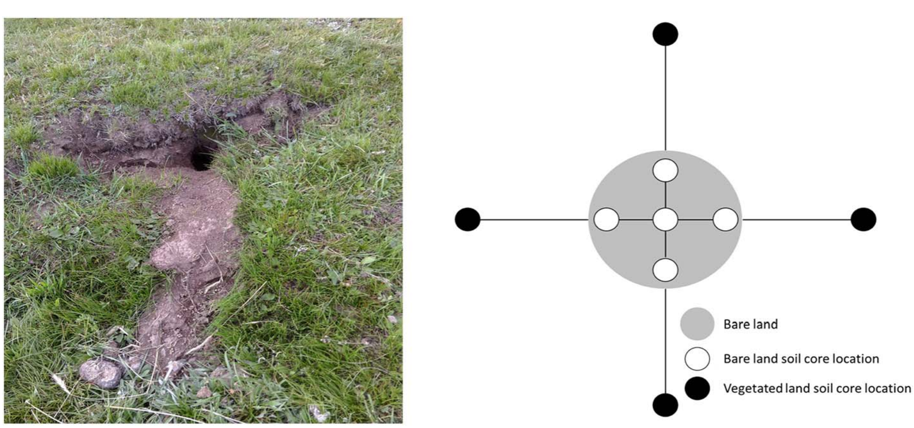

Fig. 2. Approximate orientation of soil sampling transects over each bare subplot and vegetated subplot.

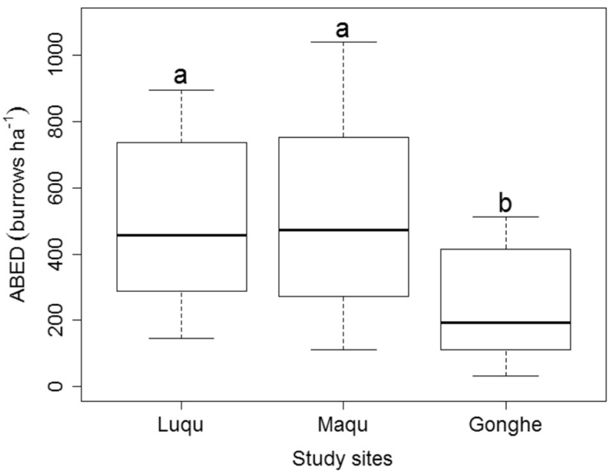

Fig. 3. Active burrow entrance densities of plateau pika in the three study sites of the QTP, China. Lower-case letters indicate significant differences among the three study sites based on a non-parametric multiple test at alpha < 0.05. ABED: active burrow entrance densities. From top to bottom of standard boxplot are the maximum, the third quartile, median, first quartile, and minimum.

576, 752, 928, and 1040 in Maqu County, and 32, 80, 112, 128, 176, 208, 240, 416, 464, and 512 in Gonghe County. The average active burrow entrances (averages ± SD) in disturbed areas were 493 ± 263 per ha in Luqu County, 520 ± 308 per ha in Muqu County, and 237 ± 169 per ha in Gonghe County. The burrow entrances were significantly different among the three study sites (Fig. 3).

3.2. Effects of disturbance caused by plateau pika bioturbation on soil nutrient concentrations

With the exception of TK and AK concentrations, the disturbances had significant effects on other nutrient concentrations measured (Tables 1 and 2). Accounting for an overall scale effect, TN, SOC and TP concentrations of bare land were significantly lower than those of vegetated land, while NO_3^--N, NH_4^+-N and AP concentrations tended to be higher of bare land than in vegetated land across the three study sites (Fig. 4).

Accounting for a site scale effect, similar responses of soil nutrient concentrations to disturbance were observed in the three study sites with the exception of TP concentrations (Table 2). The responses of TP concentrations to disturbance were site-dependent. TP concentrations in bare land were lower than in vegetated land, and the difference in TP concentrations between bare land and vegetated land was significant in Gonghe County but was not significant in Maqu County and Luqu County.

Table 1
Soil nutrients in relationship to the disturbance caused by plateau pika bioturbation in the three study sites of the *Kobresia pygmaea* meadow in the Qinghai-Tibetan Plateau (QTP), based on linear mixed models.

Response variable	Linear mixed models (site as a random factor, number of active burrows at each sample point as a covariate)					
	Site		Disturbance		Site × disturbance	
	F	p value	F	p value	F	p value
TN (g kg^{-1})	66.484	0.001	54.387	0.001	5.539	0.063
SOC (g kg^{-1})	31.977	0.009	79.459	0.001	2.860	0.239
TP (g kg^{-1})	12.605	0.002	21.259	0.001	3.713	0.156
TK (g kg^{-1})	0.618	0.734	0.555	0.456	2.492	0.28
NO_3^--N (mg kg^{-1})	2.065	0.356	96.731	0.001	0.050	0.975
NH_4^+-N (mg kg^{-1})	2.797	0.247	73.133	0.001	6.003	0.049
AP (mg kg^{-1})	24.313	0.001	73.585	0.001	3.505	0.173
AK (mg kg^{-1})	92.815	0.001	1.577	0.209	4.191	0.123

Each soil nutrient acts as a response variable while the predictors were as follows: the bare/vegetated subplots (disturbance), the three study sites (site), and the interaction of both. The factor of site acted as a random variable. TN: total nitrogen; SOC: soil organic carbon; TP: total phosphorus; TK: total potassium: AP: available phosphorus; AK: available potassium.

3.3. Effects of the disturbance intensity of plateau pika on soil nutrient concentrations

With the exception of TK and AK concentrations, other soil nutrient concentrations of bare land and vegetated land across the three sites were strongly influenced by the disturbance intensity of plateau pika (Figs. 5, 6 and 7). In Maqu County and Luqu County, TN, SOC and TP concentrations of vegetated land significantly increased at first and later decreased notably, while NO_3^--N, NH_4^+-N and AP concentrations dropped significantly at first and later increased rapidly, and the all soil nutrients of bare land slightly increased at first and subsequently sharply declined as the disturbance intensity of plateau pika increased, indicating that disturbance intensities of plateau pika had a clear threshold for *K. pygmaea* meadow. In Gonghe County, the highest active burrow entrance density was 512 per ha, and TN, SOC and TP concentrations of vegetated land significantly increased, while NO_3^--N, NH_4^+-N and AP concentrations significantly decreased, and all soil nutrients of bare land increased with the increase of disturbance intensity of plateau pika. The results from Gonghe County indirectly resembled the results from Maqu County and Luqu County, and the response of soil nutrient to the disturbance intensities of plateau pika was consistent across the three study sites.

This study also revealed a broad common pattern concerning the response of the soil nutrients of vegetated land and bare land to the disturbance intensities of plateau pika across the three study sites. With the exception of TK and AK concentrations, other soil nutrients of vegetated land and bare land showed significant unimodal curvilinearity as the disturbance intensity of the plateau pika increased (Figs. 8, 9). The threshold of disturbance intensities was 436 (436 ± 42) per ha and 362 (362 ± 105) per ha for vegetated land and bare land, respectively.

4. Discussion

Plateau pika bioturbation usually creates discrete and distinctive bare land widely distributed over the alpine meadow in the QTP (Davidson and Lightfoot, 2008; Wu et al., 2015), and this disturbance causes soil redistribution and possibly affects soil nutrient concentrations among different horizons of alpine meadow. Our results show that the disturbance caused by plateau pika bioturbation strongly affects most soil nutrient concentrations with the exception of TK and AK. Total nutrient concentrations (TN, SOC and TP) of bare land significantly decreased but available nutrient concentrations (NO_3^--N, NH_4^+-N and AP) of bare land significantly increased, and similar results also have been found in disturbance created by badgers (*Taxidea taxus*), in which total carbon and nitrogen concentrations decrease in bare land (Eldridge and Whitford, 2009).

We present several explanations for why the disturbance decreases TN and SOC concentrations of bare land. First, the decrease in the input of organic matter enables the TN and SOC concentrations to reduce because the vegetation cover and biomass of bare land is absent (Zhang et al., 2016). Second, the deep layer soils with low organic substances have been carried to overlay the original topsoil in the process of soil turnover, which contributes to the reduction of TN and SOC concentrations (Kurek et al., 2014). Finally, plant materials on the surface are subject to abiotic breakdown by ultraviolet light, and they are subsequently lost from the ecosystem through comminution by the wind and thus will not return to the topsoil, making them unavailable

Table 2
Soil nutrient concentrations (mean ± standard deviation) of bare land and vegetated land in Maqu County, Luqu County and Gonghe County of the QTP.

Nutrients (unites)	Maqu County		p value	Luqu County		p value	Gonghe County		p value
	Bare land	Vegetated land		Bare land	Vegetated land		Bare land	Vegetated land	
TN (g kg^{-1})	1.90 ± 0.21	2.24 ± 0.16	0.001	2.23 ± 0.30	3.00 ± 0.37	0.000	2.67 ± 0.20	3.39 ± 0.60	0.002
SOC (g kg^{-1})	34.22 ± 4.44	42.92 ± 4.52	0.000	41.20 ± 2.85	47.13 ± 3.43	0.001	41.03 ± 3.74	50.52 ± 4.06	0.000
TP (g kg^{-1})	0.43 ± 0.11	0.48 ± 0.08	0.280	0.38 ± 0.05	0.42 ± 0.07	0.105	0.40 ± 0.04	0.51 ± 0.07	0.005
TK (g kg^{-1})	21.33 ± 1.90	22.29 ± 3.59	0.579	22.18 ± 2.92	20.41 ± 3.44	0.280	22.05 ± 2.43	21.27 ± 3.03	0.684
NO_3^--N (mg kg^{-1})	21.06 ± 3.71	13.91 ± 1.85	0.000	19.89 ± 3.95	13.10 ± 2.96	0.002	21.93 ± 2.20	14.86 ± 2.75	0.000
NH_4^+-N (mg kg^{-1})	17.02 ± 2.08	10.81 ± 3.33	0.000	14.59 ± 1.62	11.13 ± 1.51	0.001	15.15 ± 1.77	11.55 ± 1.83	0.001
AP (mg kg^{-1})	19.91 ± 2.42	16.15 ± 1.22	0.001	19.46 ± 2.83	14.73 ± 1.79	0.001	18.05 ± 3.05	11.67 ± 2.73	0.000
AK (mg kg^{-1})	182.65 ± 15.93	179.72 ± 17.58	0.481	194.93 ± 9.03	197.17 ± 12.57	0.796	216.70 ± 19.51	229.22 ± 16.57	0.130

Significant differences between the bare land and vegetated land were tested by using a Wilcoxon-Mann-Whitney test. TN: total nitrogen; SOC: soil organic carbon; TP: total phosphorus; TK: total potassium: AP: available phosphorus; AK: available potassium.

to the microbes and microarthropods and hence contributing little to the soil nutrient pools (Eldridge et al., 2009; James et al., 2009). The reason that the disturbance decreases the TP concentration of bare land rather than the TK concentration is related to in TP and TK components. TP and TK are mainly dependent on the soil parent material, and TP mainly consists of inorganic and organic phosphorus. The disturbance reduces the soil organic material, and accordingly decreases the accumulation of organic phosphorus concentration of bare land (Malizia et al., 2000; Liu et al., 2005), which contributes to reduction of TP. The TK concentration in soil organic material is much lower than that in the soil parent material (Liu et al., 2005), inferring that the decrease of the input of soil organic material contributes little to TK concentration. Therefore, the disturbance produced by plateau pika bioturbation decreases TP concentrations, while it has no effect on TK concentration under the same soil parent material conditions.

Although dead roots and litter are stored in the form of organic matter, the extremely cool climate in the study areas causes this organic matter to decompose slowly (Gong, 2001), resulting in a relatively low availability of nutrients to plants. Our findings show that the disturbance simultaneously increases the availability of soil NO_3^--N, NH_4^+-N and AP of bare land, which is in agreement with results from other studies of bioturbation of small burrowing mammals, such as pocket gopher (Canals et al., 2003) and plateau zokor (Zhang et al., 2014), arctic fox (Gharajehdaghipour et al., 2016) and pack rats (Whitford and Steinberger, 2010). These suggest that disturbance manifests the breakup the original balance of soil nutrient mineralization, which is conducive to the formation of productive soil that has nutrients available to plants. There are several reasons that disturbance increases available nutrient concentrations. First, disturbance increases soil moisture and oxygenation (lower soil hardness) of bare land (Malizia et al., 2000; Guo et al., 2012) by breaking up stable aggregates of soil particles (Canals et al., 2003; Zhang et al., 2016), which increases the nitrogen mineralization rate, resulting in higher available nitrogen concentrations of bare land; second, greater mixing of soil and

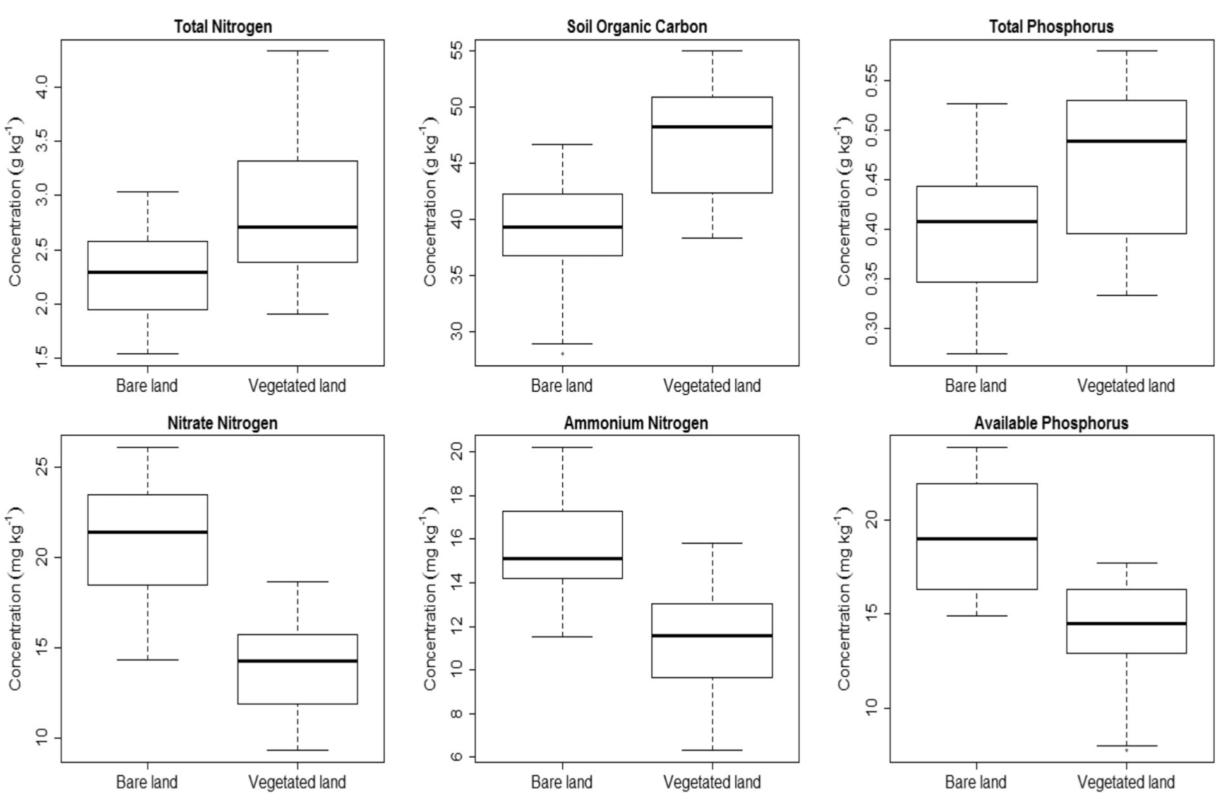

Fig. 4. Concentrations of the significant soil nutrients that differ in bare land and vegetated land according to the plateau pika bioturbation. The values were obtained from the linear mixed models with respect to the disturbance by plateau pika bioturbation in the *Kobresia pygmaea* meadow across the three study sites (see Table 2 for details). From top to bottom of standard boxplot are the maximum, the third quartile, median, first quartile, and minimum.

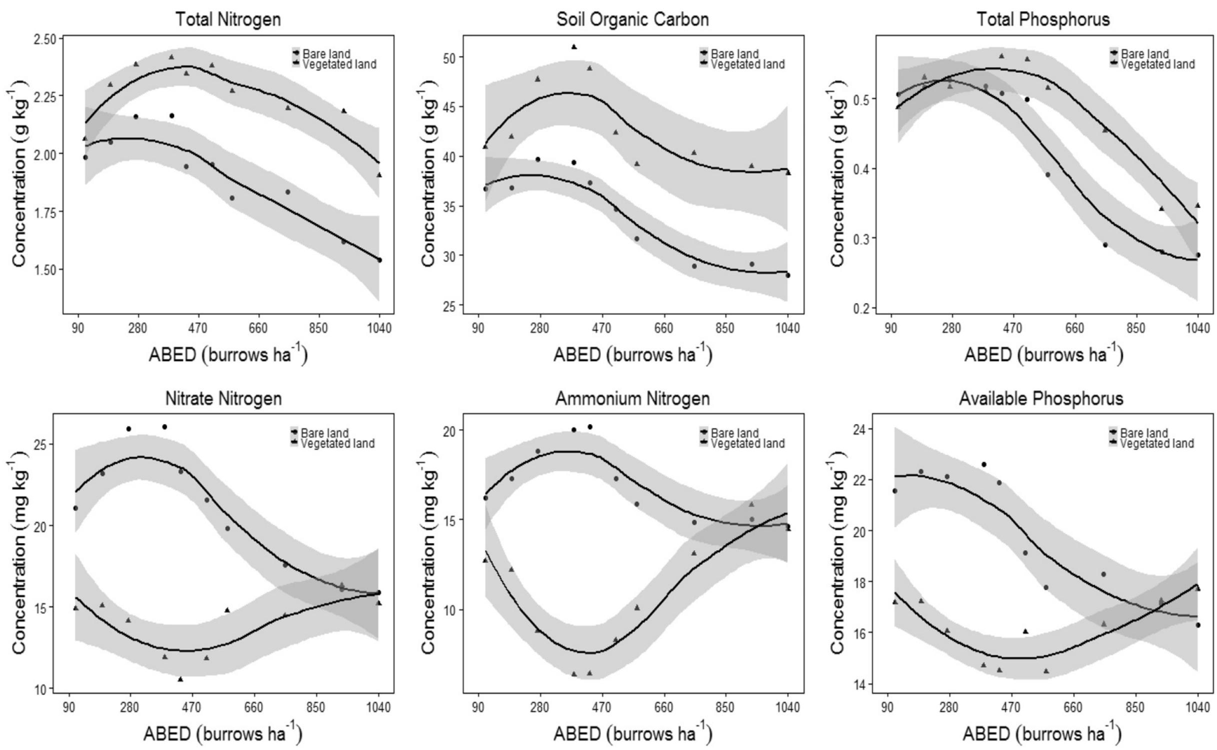

Fig. 5. Soil nutrient concentrations of bare land and vegetated land for different disturbance intensities of plateau pika in Maqu County were based on LOESS model. For a detailed visualization of the relationship between the disturbance intensity and soil nutrient concentrations, an adjusted local smoothed regression line (black) with its 95% confident interval (gray) was used. ABED: active burrow entrance densities.

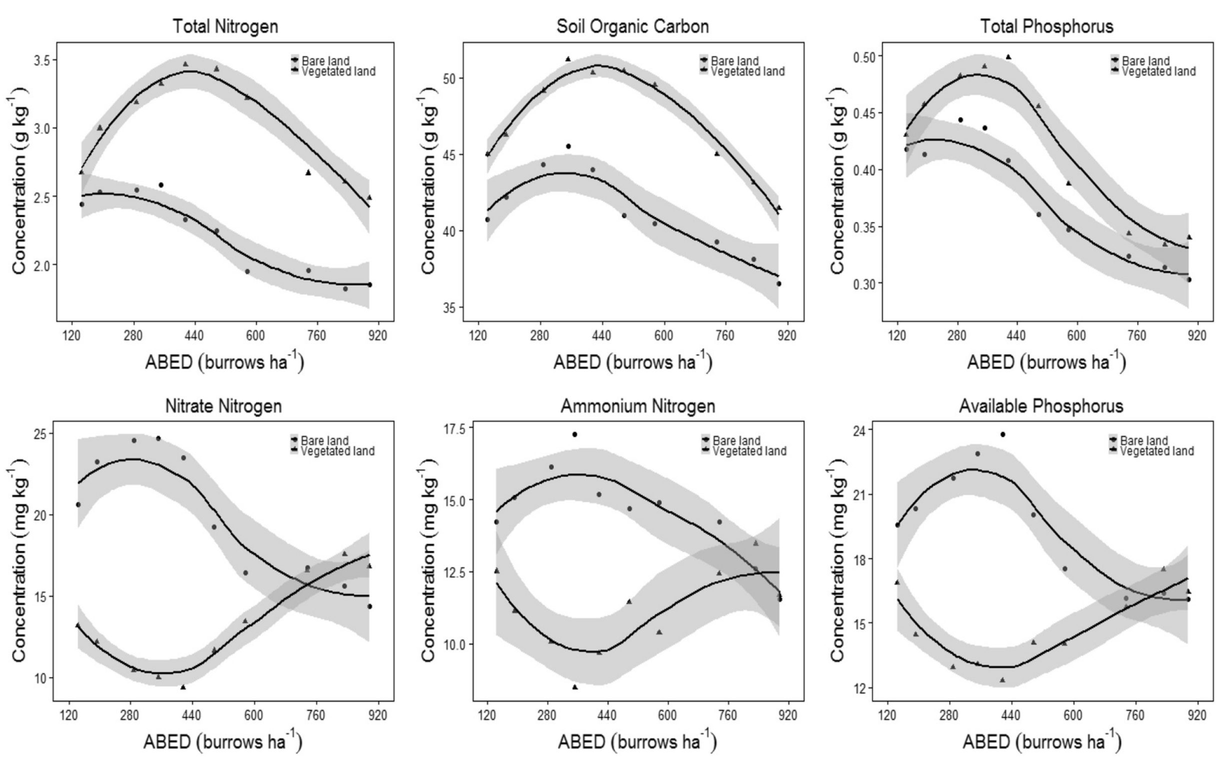

Fig. 6. Soil nutrient concentrations of bare land and vegetated land for different disturbance intensities of plateau pika in Luqu County were based on LOESS model. For a detailed visualization of the relationship between the disturbance intensity and soil nutrient concentrations, an adjusted local smoothed regression line (black) with its 95% confident interval (gray) was used. ABED: active burrow entrance densities.

litter in the developing process of bare land will be beneficial to closely contacting soil-borne fungi and micro-arthropods with litter (James et al., 2009), which is an effective means of causing litter to be decomposed by microbes, theoretically forming more soil available nutrients; third, the excretion activity of plateau pika is likely to compensate or increase somewhat the available N and P of bare land because small burrowing mammals excrete more frequency near burrow entrances (Willott et al., 2000; Hutchings et al., 2001; Kurek et al.,

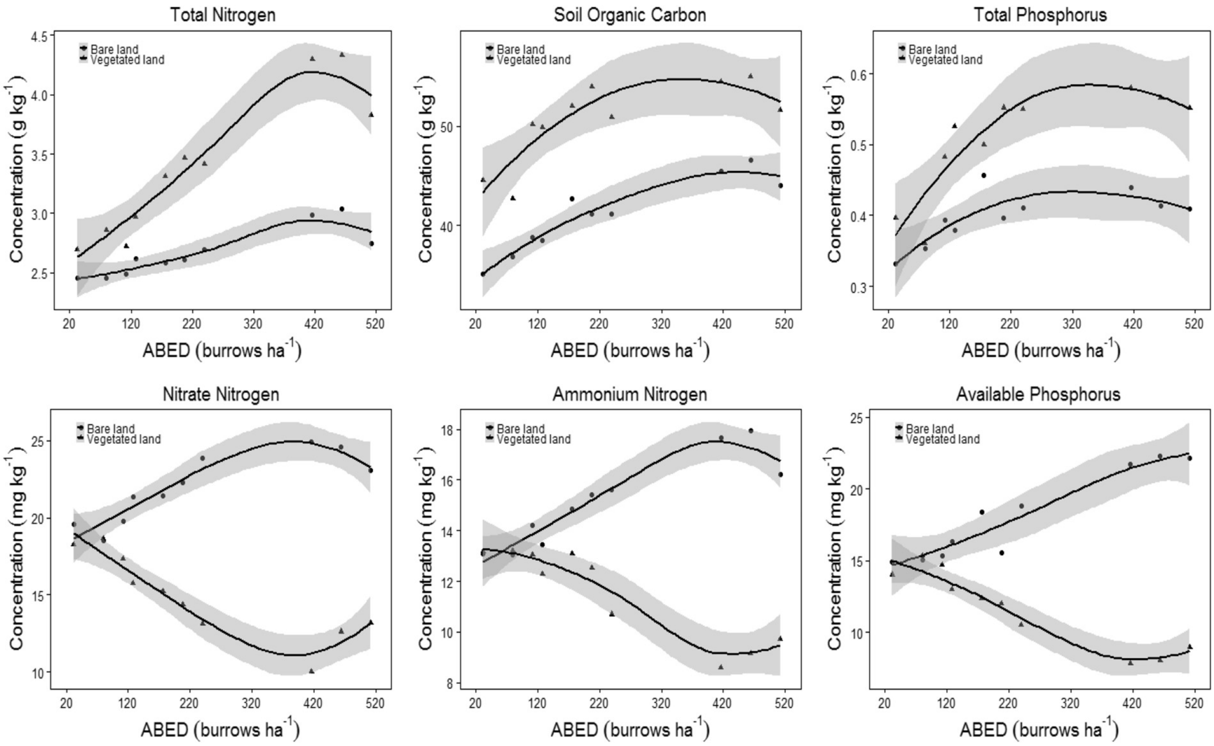

Fig. 7. Soil nutrient concentrations of bare land and vegetated land for different disturbance intensities of plateau pika in Gonghe County were based on LOESS model. For a detailed visualization of the relationship between the disturbance intensity and soil nutrient concentrations, an adjusted local smoothed regression line (black) with its 95% confident interval (gray) was used. ABED: active burrow entrance densities.

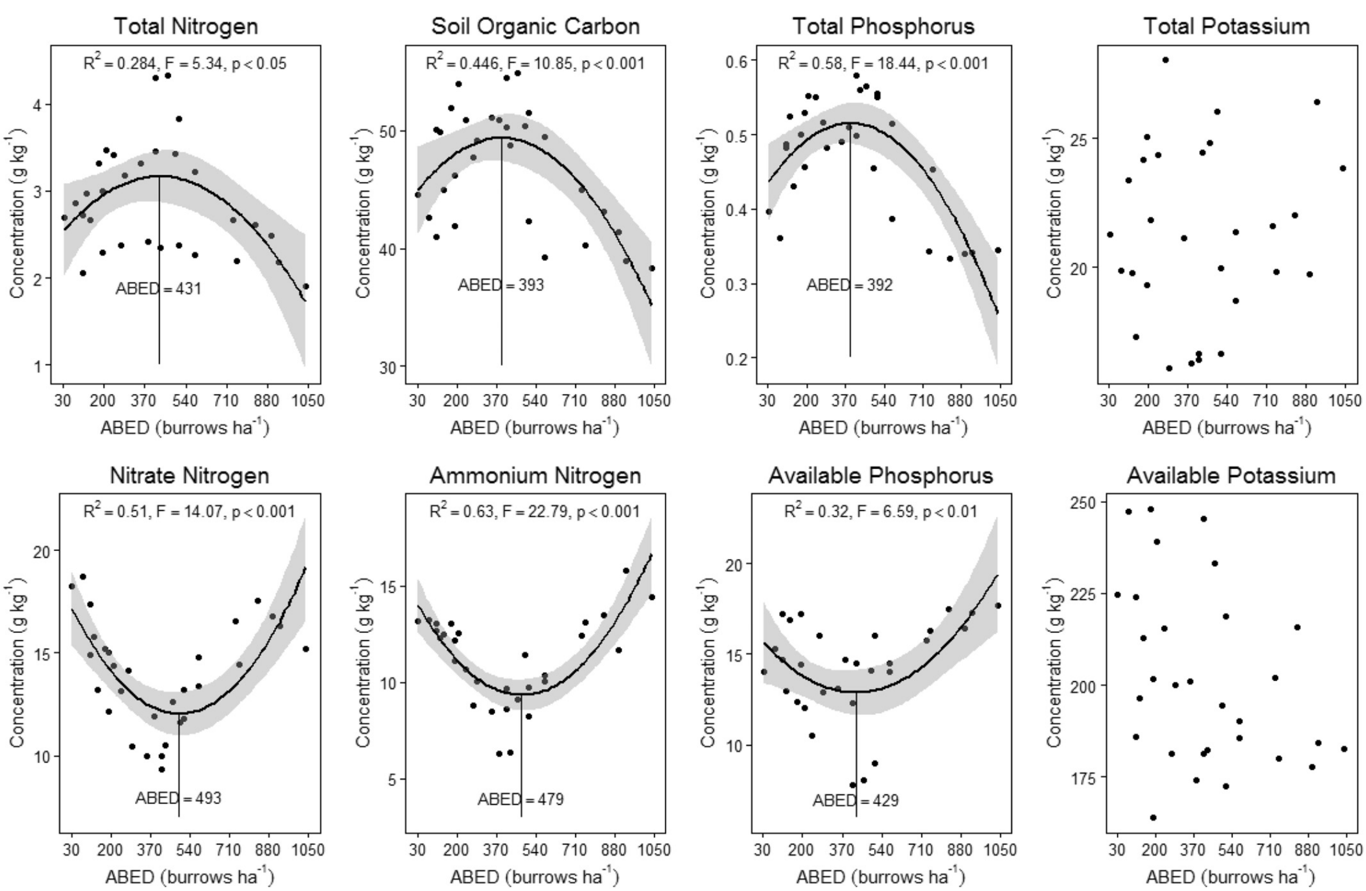

Fig. 8. Soil nutrient concentrations of vegetated land for different disturbance intensities of plateau pika across the three study sites were based on linear model (LM). For a detailed visualization of the relationship between the disturbance intensity and soil nutrient concentrations, an adjusted local smoothed regression line (black) with its 95% confident interval (gray) was used. ABED: active burrow entrance densities.

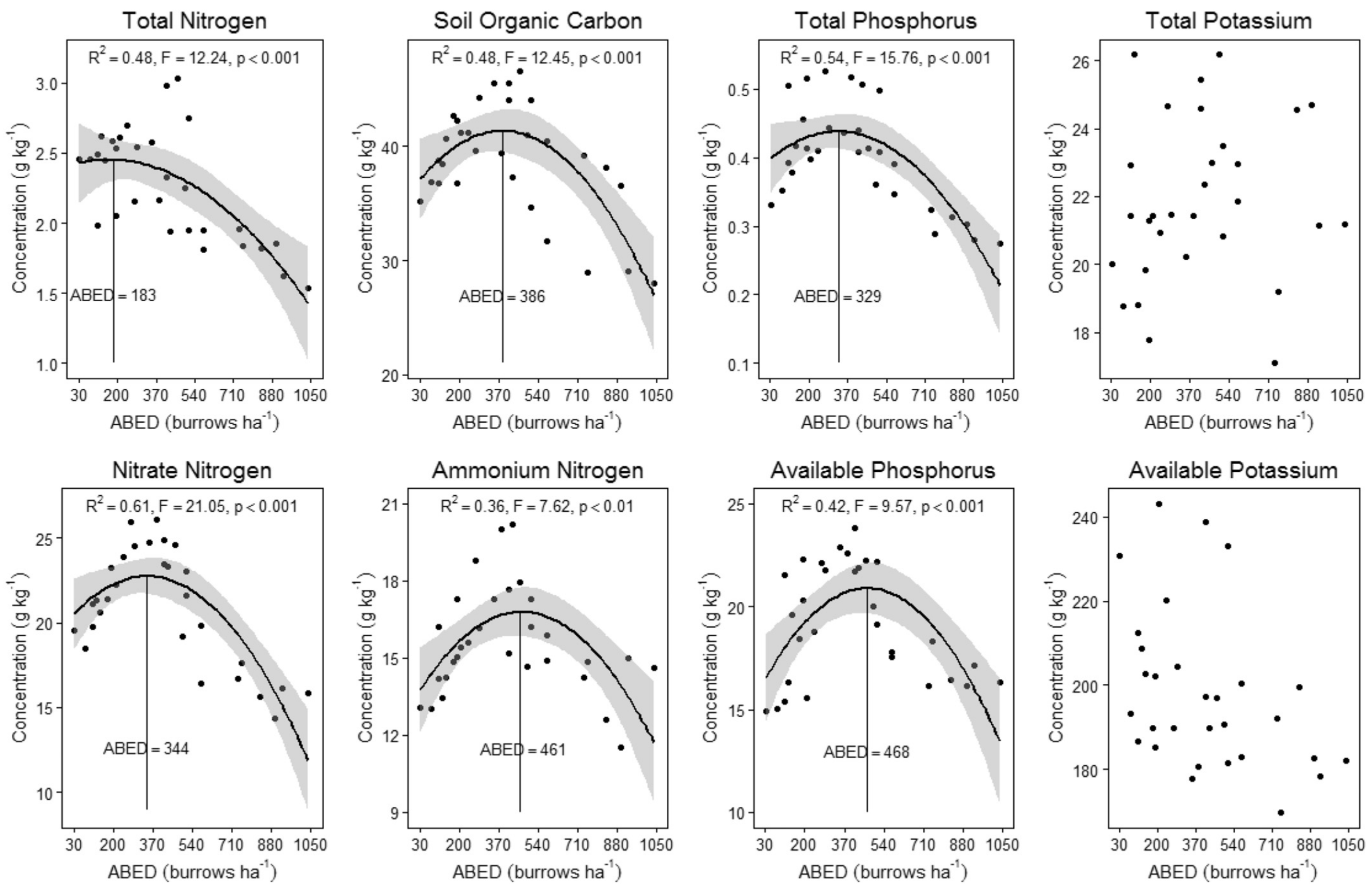

Fig. 9. Soil nutrient concentrations of bare land for different disturbance intensities of plateau pika across the three study sites were based on LM. For a detailed visualization of the relationship between the disturbance intensity and soil nutrient concentrations, an adjusted local smoothed regression line (black) with its 95% confident interval (gray) was used. ABED: active burrow entrance densities.

2014). Available nutrient accumulation of bare land often make bare land develops a “fertile island” with higher nitrogen and phosphorus concentrations (Malizia et al., 2000; Galiano et al., 2014; Yurkewycz et al., 2014), which provides good habitat and “safe sites” for the growth of rare plant species and the nitrophilous graminoid plants, many of which are high in crude protein and digestibility (Fleming et al., 2014; Wu et al., 2015; Gharajehdaghipour et al., 2016). To a certain extent, higher available nutrient concentrations of topsoil developed by plateau pika bioturbation will improve the grazing quality and maintain high plant diversity of alpine meadow in the QTP.

Our study further found that the effect of the disturbance caused by plateau pika on soil nutrient concentrations is closely related to the disturbance intensities of plateau pika. TN, SOC and TP are significantly higher at moderate disturbance intensities of plateau pika than that at low or high disturbance intensities both in vegetated land and bare land. These results suggest that the appropriate disturbance intensity is conducive to maximize the storage of soil carbon, nitrogen and phosphorus pools, and this was also reported for the Guoluo regions in the QTP (Guo et al., 2012; Sun et al., 2015a). In vegetated land, plateau pika disturbance within its threshold improved the physical and chemical properties of surface soil (Guo et al., 2012; Dong et al., 2013; Yu et al., 2017), encouraging microorganisms to decompose litter and dead roots, which contributes to the increase of TN, SOC and TP. When the disturbance intensity is over its threshold, the decrease in the input of organic matter, resulting from low vegetation biomass (Liu et al., 2013; Sun et al., 2015a), reduces the TN, SOC and TP concentrations. In bare land, TN, SOC and TP concentrations show a slightly increasing trend when the disturbance intensity is below its threshold. For a small amount of bare land, vegetation near the bare land has a buffer function to maintain the TN, SOC and TP of the bare land (Guo et al., 2012), and the urine and fecal deposition of plateau pika contributes to increases of TN, SOC and TP concentrations (James et al., 2009). The responses of available nutrient concentrations to the disturbance intensity of plateau pika are different between vegetated land and bare land. Our findings show that moderate disturbance intensities significantly decrease NO_3^--N, NH_4^+-N and AP concentrations of vegetated land, while high disturbance intensities significantly decrease NO_3^--N, NH_4^+-N and AP concentrations of bare land. In vegetated land, this finding may be ascribed to moderate disturbance intensities improving plant biomass near burrow entrances when compared to the control sites (without plateau pika burrows) (Zhang et al., 2016), and higher plant absorption and utilization may contribute to a decrease in available nutrient concentration of topsoil (Galiano et al., 2014). In bare land, high disturbance intensities of plateau pika reduce the vegetation cover and increase the bare land area (Qi et al., 2008; Dong et al., 2013), where the shortage of vegetation buffer and the low utilization of plants collectively reduce the available nutrients concentration of topsoil.

The responses of the main soil nutrient concentrations to the disturbance intensity of plateau pika in this study are different from the results from the Three Rivers Headwaters region (Liu et al., 2013; Peng et al., 2015) and Guoluo regions (Guo et al., 2012; Sun et al., 2015a), in which alpine meadow types or bare land have been not considered in the process of collecting soil samples. Therefore, studies of the responses of the main soil nutrient concentrations to the plateau pika bioturbation should choose the same alpine meadow to avoid the effects of different alpine meadow types on soil nutrient concentrations; meanwhile, we should consider the effect of the disturbance on the soil nutrient concentrations by choosing an appropriate scale.

5. Conclusions

Our results show that the disturbance within the threshold of disturbance intensity of plateau pika is beneficial to the storage of soil carbon and nitrogen pools. The increase of available soil nitrogen (NO_3^--N, NH_4^+-N) in the QTP will optimize the grazing quality and keep high plant diversity of alpine meadow by providing good habitats for some rare plants and supplying nutrients for the nitrophilous graminoid plants to grow well in bare land. When the disturbance intensity is over the threshold, the beneficial effectiveness of the disturbance will weaken for alpine meadow. These results will help to elucidate the role of plateau pika in the alpine meadow ecosystem of the QTP and to provide comprehensive information regarding plateau pika bioturbation influencing the soil nutrient concentrations.

Acknowledgments

This research was funded by the National Key Research and Development Program of China (No. 2016YFC0502005), the National Natural Science Foundation of China (No. 31172258), and the Fundamental Research Funds for Central Universities of Lanzhou University, China (No. lzujbky-2016-189 and lzujbky-2016-190).

References

Bates, D.M., 2005. Fitting linear mixed models in R. R News 5, 27–30.
Bueno, C.G., Azorín, J., Gómez-García, D., Alados, C.L., Badía, D., 2013. Occurrence and intensity of wild boar disturbances, effects on the physical and chemical soil properties of alpine grasslands. Plant Soil 373, 243–256.
Canals, R.M., Herman, D.J., Firestone, M.K., 2003. How disturbance by fossorial mammals alters N cycling in California annual grassland. Ecology 84, 875–881.
Chen, J.J., Yi, S.H., Qin, Y., 2017. The contribution of plateau pika disturbance and erosion on patchy alpine grassland soil on the Qinghai-Tibetan Plateau: implications for grassland restoration. Geoderma 297, 1–9.
Davidson, A.D., Lightfoot, D.C., 2008. Burrowing rodents increase landscape heterogeneity in a desert grassland. J. Arid Environ. 72, 1133–1145.
Delibes-Mateos, M., Smith, A.T., Slobodchikoff, C.N., Swenson, J.E., 2011. The paradox of keystone species persecuted as pests: a call for the conservation of abundant small mammals in their native range. Biol. Conserv. 144, 1335–1346.
Desoky, A.E.A.S.S., 2015. The most important methods used to estimate the population density of rodents. World J. Agric. Biol. Sci. 2, 1–6.
Dong, Q.M., Zhao, X.Q., Wu, G.L., Shi, J.J., Ren, G.H., 2013. A review of formation mechanism and restoration measures of "black-soil-type" degraded grassland in the Qinghai-Tibetan Plateau. Environ. Earth Sci. 70, 2359–2370.
Eldridge, D.J., Whitford, W.G., 2009. Badger (*Taxidea taxus*) disturbances increase soil heterogeneity in a degraded shrub-steppe ecosystem. J. Arid Environ. 73, 66–73.
Eldridge, D.J., Whitford, W.G., Duval, B.D., 2009. Animal disturbances promote shrub maintenance in a desertified grassland. J. Ecol. 97, 1302–1310.
Escobedo, V.M., Rios, R.S., Salgado-Luarte, C., Stotz, G.C., Gianoli, E., 2017. Disturbance by an endemic rodent in an arid shrubland is a habitat filter: effects on plant invasion and taxonomical, functional and phylogenetic community structure. Ann. Bot. 119, 659–670.
Fleming, P.A., Anderson, H., Prendergast, A.S., Bretz, M.R., Valentine, L.E., Hardy, G.E.S., 2014. Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function? Mammal Rev. 44, 94–108.
Galiano, D., Kubiak, B.B., Overbeck, G.E., de Freitas, T.R.O., 2014. Effects of rodents on plant cover, soil hardness, and soil nutrient content: a case study on tuco-tucos (*Ctenomys minutus*). Acta Theriol. 59, 583–587.
García-González, R., 2008. Management of natura 2000 habitats. Alpine and subalpine calcareous grasslands 6170. In: Technical Report. 2008 (11/24).
Gharajehdaghipour, T., Roth, J.D., Fafard, P.M., Markham, J.H., 2016. Arctic foxes as ecosystem engineers: increased soil nutrients lead to increased plant productivity on fox dens. Sci Rep 6, 24020.
Gong, Z., 2001. Chinese Soil Taxonomy. Sci. Press, China.
Guo, Z.G., Zhou, X.R., Hou, Y., 2012. Effect of available burrow densities of plateau pika (*Ochotona curzoniae*) on soil physicochemical property of the bare land and vegetation land in the Qinghai-Tibetan Plateau. Acta Ecol. Sin. 32, 104–110.
Hutchings, M.R., Hutchings, M.R., Harris, S., 2001. Defecation and urination patterns of badgers *Meles meles* at low density in south west England. Acta Theriol. 46, 87–96.
James, A.I., Eldridge, D.J., Hill, B.M., 2009. Foraging animals create fertile patches in an Australian desert shrubland. Ecography 32, 723–732.
Kabacoff, R.I., 2011. R in Action: Data Analysis and Graphics with R. Manning Publications.
Körner, C., 2003. Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems; With 47 Tables. Springer Sci. Bus. Media.
Kurek, P., Kapusta, P., Holeksa, J., 2014. Burrowing by badgers (*Meles meles*) and foxes (*Vulpes vulpes*) changes soil conditions and vegetation in a European temperate forest. Ecol. Res. 29, 1–11.
Lai, C.H., Smith, A.T., 2003. Keystone status of plateau pikas (*Ochotona curzoniae*): effect of control on biodiversity of native birds. Biodivers. Conserv. 12, 1901–1912.
Liu, S.Q., Gao, L.L., Pu, Y.L., Deng, L.J., Zhang, S.R., 2005. Status of soil P and K nutrient and their influencing factors in Tibet. J. Soil Water Conserv. 19, 75–78 (in Chinese with English abstract).
Liu, Y.S., Fan, J.W., Harris, W., Shao, Q.Q., Zhou, Y.C., Wang, N., Li, Y.Z., 2013. Effects of plateau pika (*Ochotona curzoniae*) on net ecosystem carbon exchange of grassland in the Three Rivers Headwaters region, Qinghai-Tibet, China. Plant Soil 366, 491–504.
Liu, Y.S., Fan, J.W., Shi, Z.J., Yang, X.H., Harris, W., 2017. Relationships between plateau pika (*Ochotona curzoniae*) densities and biomass and biodiversity indices of alpine meadow steppe on the Qinghai–Tibet Plateau China. Ecol. Eng. 102, 509–518.
Malizia, A.I., Kittlein, M.J., Busch, C., 2000. Influence of the subterranean herbivorous rodent *Ctenomys talarum* on vegetation and soil. Z. Säugetierkd. 65, 172–182.
Moore, D.S., McCabe, G.P., Craig, B., 2008. Introduction to the Practice of Statistics. W.H Freemanpp. 100.
Nelson, D.W., Sommers, L., 1982. Total carbon, organic carbon, and organic matter. Methods of soil analysis. In: Part 3- Chemical and Microbiological Properties, pp. 539–579.
Pang, X.P., Guo, Z.G., 2017. Plateau pika disturbances alter plant productivity and soil nutrients in alpine meadows of the Qinghai-Tibetan Plateau, China. Rangel. J. 39, 133–144.
Peng, F., Quangang, Y., Xue, X., Guo, J., Wang, T., 2015. Effects of rodent-induced land degradation on ecosystem carbon fluxes in an alpine meadow in the Qinghai–Tibet Plateau, China. Solid Earth 6, 303–310.
Qi, D.C., Chen, W.Y., Zheng, H.P., Li, G.Y., Liu, Z.H., Zong, W.J., 2008. Status, causes and comprehensive treatment of "black beach like" degraded pasture in water replenishment region of upper Yellow River in south of Gansu province. J. Desert Res. 28, 1058–1063 (in Chinese with English abstract).
Reichmana, O.J., Seabloomb, E.W., 2002. The role of pocket gophers as subterranean ecosystem engineers. Trends Ecol. Evol. 17, 44–49.
Schooley, R.L., Bestelmeyer, B.T., 2000. Influence of small-scale disturbances by kangaroo rats on Chihuahuan Desert ants. Oecologia 125, 142–149.
Smith, A.T., Foggin, J.M., 1999. The plateau pika (*Ochotona curzoniae*) is a keystone species for biodiversity on the Tibetan plateau. Anim. Conserv. 2, 235–240.
Smith, A.T., Gao, W.X., 1991. Social relationships of adult black-lipped pikas (*Ochotona curzoniae*). J. Mammal. 72, 231–247.
Sun, F.D., Chen, W.Y., Liu, L., Liu, W., Cai, Y.M., Smith, P., 2015a. Effects of plateau pika activities on seasonal plant biomass and soil properties in the alpine meadow ecosystems of the Tibetan Plateau. Grassl. Sci. 61, 195–203.
Sun, F.D., Chen, W.Y., Liu, L., Liu, W., Lu, C.X., Smith, P., 2015b. The density of active burrows of plateau pika in relation to biomass allocation in the alpine meadow ecosystems of the Tibetan Plateau. Biochem. Syst. Ecol. 58, 257–264.
Villarreal, D., Clark, K.L., Branch, L.C., Hierro, J.L., Machicote, M., 2008. Alteration of ecosystem structure by a burrowing herbivore, the plains vizcacha (*Lagostomus maximus*). J. Mammal. 89, 700–711.
Wangdwei, M., Steele, B., Harris, R.B., 2013. Demographic responses of plateau pikas to vegetation cover and land use in the Tibet Autonomous Region, China. J. Mammal. 94, 1077–1086.
Wei, X.H., Li, S., Yang, P., Cheng, H.S., 2007. Soil erosion and vegetation succession in alpine *Kobresia* steppe meadow caused by plateau pika—a case study of Nagqu County, Tibet. Chin. Geogr. Sci. 17, 75–81.
Whitford, W.G., Steinberger, Y., 2010. Pack rats (*Neotoma* spp.): keystone ecological engineers? J. Arid Environ. 74, 1450–1455.
Wilkinson, M.T., Richards, P.J., Humphreys, G.S., 2009. Breaking ground: pedological, geological, and ecological implications of soil bioturbation. Earth Sci. Rev. 97, 257–272.
Willott, S.J., Miller, A.J., Incoll, L.D., Compton, S.G., 2000. The contribution of rabbits (*Oryctolagus cuniculus* L.) to soil fertility in semi-arid Spain. Biol. Fertil. Soils 31, 379–384.
Wilson, M.C., Smith, A.T., 2015. The pika and the watershed: the impact of small mammal poisoning on the ecohydrology of the Qinghai-Tibetan Plateau. Ambio 44, 16–22.
Wu, R.X., Chai, Q., Zhang, J.Q., Zhong, M.Y., Liu, Y.H., Wei, X.T., Pan, D., Shao, X.Q., 2015. Impacts of burrows and mounds formed by plateau rodents on plant species diversity on the Qinghai-Tibetan Plateau. Rangel. J. 37, 117–123.
Xu, W.X., Liu, W., Yang, W.K., Tang, C.W., Blank, D., 2012. *Rhombomys opimus* contribution to the "fertile island" effect of tamarisk mounds in Junggar Basin. Ecol. Res. 27, 775–781.
Yu, C., Jia, T.T., Pang, X.P., Guo, Z.G., 2016. Effects of plateau pika (*Ochotona Curzoniae*) disturbing soil carbon and nitrogen distribution in alpine meadow. Acta Pedol. Sin. 53, 208–218 (in Chinese with English abstract).
Yu, C., Pang, X.P., Wang, Q., Jin, S.H., Shu, C.C., Guo, Z.G., 2017. Soil nutrient changes induced by the presence and intensity of plateau pika (*Ochotona curzoniae*) disturbances in the Qinghai-Tibet Plateau, China. Ecol. Eng. 106, 1–9.
Yurkewycz, R.P., Bishop, J.G., Crisafulli, C.M., Harrison, J.A., Gill, R.A., 2014. Gopher mounds decrease nutrient cycling rates and increase adjacent vegetation in volcanic primary succession. Oecologia 176, 1135–1150.
Zhang, W., Liu, C.Y., Zheng, X.H., Fu, Y.F., Hu, X.X., Cao, G.M., Butterbach-Bahl, K., 2014. The increasing distribution area of zokor mounds weaken greenhouse gas uptakes by alpine meadows in the Qinghai–Tibetan Plateau. Soil Biol. Biochem. 71, 105–112.
Zhang, Y., Dong, S.K., Gao, Q.Z., Liu, S.L., Liang, Y., Cao, X.J., 2016. Responses of alpine vegetation and soils to the disturbance of plateau pika (*Ochotona curzoniae*) at burrow level on the Qinghai–Tibetan Plateau of China. Ecol. Eng. 88, 232–236.
Zhou, X.R., Guo, Z.G., Guo, X.H., 2010. The role of plateau pika and plateall zokor in alpine meadow. Pratac. Sci. 27, 38–44 (in Chinese with English abstract).