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ORIGINAL ARTICLE

Effects of small-herbivore disturbance on the clonal growth of two perennial graminoids in alpine meadows

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Abstract
Graminoids are typically the dominant plants in certain grassland communities, and their clonal growth is considered an important method of evaluating their adaptation to environmental disturbances. Whether disturbances caused by small burrowing herbivores influence clonal growth in graminoids is not well documented. A field experiment was conducted to investigate the effects of disturbances by small burrowing herbivores, the plateau pika, on the clonal growth of the tussock-forming *Kobresia pygmaea* and the rhizomatous *K. humilis* across three sites. This study showed that disturbance by plateau pikas increased the shoot number, spacer number and tiller bud number per clonal fragment of both the tussock-forming *K. pygmaea* and the rhizomatous *K. humilis* across three sites. This study also showed that disturbance by plateau pikas increased the rhizome branch number, rhizome length, and rhizome bud number per clonal fragment of rhizomatous *K. humilis* at each site, while the effects of disturbance by plateau pikas on the rhizome branch number, rhizome length, and rhizome bud number per clonal fragment of the tussock-forming *K. pygmaea* were different among the three sites. These results suggested that disturbance by plateau pikas benefits for current and potential population recruitment in the tussock-forming *K. pygmaea* and the rhizomatous *K. humilis* due to the resulting higher shoot number and tiller bud number per clonal fragment.

Keywords Clonal growth · Tussock-forming plant · Rhizomatous plant · Alpine meadow · Plateau pika disturbances

Introduction

Most natural grasslands are dominated by perennial graminoids (Gibson 2009). The reproduction of dominant perennial graminoids often shapes plant community succession (Pottier and Evette 2010) by regulating the population regeneration of these graminoids (Rusch et al. 2010). The dominant perennial graminoids mainly use vegetative reproduction to assemble their population and regenerate in natural grasslands (Benson and hartnett 2006; Gao et al. 2012), since thick grassland litter often limits seed germination, seedling emergence and establishment (Benson and Hartnett 2006; VanderWeide and Hartnett 2015). As a key vegetative reproduction trait, clonal growth can encourage dominant perennial graminoids to colonize rapidly because clonal growth plants naturally and quickly produce offspring and ramets with potential clonal fragments in habitats disturbed by biotic factors (Wang et al. 2004; Benot et al. 2011a; Ott and Hartneet 2014; Herben et al. 2015; Johansen et al. 2016). Therefore, examining the effects of biotic disturbances on the clonal growth of dominant perennial graminoids is necessary to understand the contribution of these disturbances to plant community succession in grassland (Jinhua et al. 2010; Benot et al. 2011a; Qian et al. 2014).

Herbivores are an important component of grassland ecosystems (Bakker et al. 2006; Van Staalduinen and Werger 2007; Davidson et al. 2012; Smith et al. 2019). The interactions between herbivores and graminoids are reciprocal (Davidson et al. 2012; Jia et al. 2018); herbivores often consume graminoids, which suppress graminoid growth (Bakker

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et al. 2006), but the consumption by herbivores can, in turn, stimulate compensatory graminoid growth (Mcnaughton 1983; Zhang et al. 2020) leading to higher tiller productions (Wang et al. 2018). Clonal growth in graminoids can usually be estimated by various clonal traits and bud bank traits (Jinhua et al. 2010; Klimešová et al. 2016; Johansen et al. 2016; Ott and Hartnett 2014). Currently, large-herbivore grazing has been demonstrated to alter the clonal traits (Jinhua et al. 2010; Benot et al. 2011a) and bud bank traits (Fidelis et al. 2014; Qian et al. 2014) of perennial graminoid plants. In addition to large herbivores, small burrowing herbivores are also important components of most grassland ecosystems (Davidson et al. 2012). Tens to thousands of small burrowing herbivores can create extensive disturbances in grassland plant communities (Liu et al. 2017; Smith et al. 2019). Their disturbances can alter the degree of dominance of one plant species (Pang and Guo 2018), the plant species richness (Davidson et al. 2012; Smith et al. 2019; Zhang et al. 2020) and the biomass of plant functional groups (Liu et al. 2017; Pang and Guo 2017). This suggests that disturbances by small burrowing herbivores may influence the clonal growth of dominant perennial graminoids.

Plateau pikas (*Ochotona curzoniae*) are small burrowing herbivores that are common in the vast alpine meadows of the Qinghai-Tibetan Plateau (Smith et al. 2019). In these alpine meadows, dominant perennial graminoids usually regenerate their populations through clonal growth, rather than seed reproduction (Wang et al. 2018) due to low temperatures, short growing seasons and a thick litter layer (Klimešová et al. 2011). Although the clonal growth of perennial graminoids mainly includes tussock, rhizomatous and stoloniferous forms (Gough et al. 2001; Zheng et al. 2019), the stoloniferous growth form is not common in alpine meadows with high soil organic matter (Fang et al. 2014), and this form is mainly observed in barren soil habitats (Jinhua et al. 2010). Therefore, the main clonal growth forms in alpine meadows of the Qinghai-Tibetan Plateau are tussock-forming and rhizomatous. Disturbance by plateau pikas has direct and indirect impacts on perennial graminoids growth (Sun et al. 2015; Smith et al. 2019). Plateau pikas preferentially consume aboveground parts of perennial graminoids (Pang and Guo 2017) and clip perennial graminoids (Zhang et al. 2020), and this consumption can induce plant compensation growth (Mcnaughton 1983), which facilitates plant rhizome growth. In addition, plateau pika disturbance can increase the soil nitrogen concentration (Yu et al. 2017; Pang et al. 2020), which is beneficial to perennial graminoid rhizome growth, because some perennial graminoids are nitrophiles (Zheng et al. 2019). Additionally, it is now well established that disturbance by plateau pikas can increase the ratio of vegetative shoots to reproductive shoots in one plant (Zhang et al. 2018) and increase the perennial graminoid biomass (Pang and Guo 2017). However, whether disturbance by plateau pikas influences the clonal growth of tussock-forming plants and rhizomatous plants is not well documented.

Kobresia pygmaea is a dominant plant with a tussock clonal growth form, and *K. humilis* is a common plant with a rhizomatous clonal growth form in alpine meadows of the Qinghai-Tibetan Plateau (Wang et al. 2012; Fang et al. 2014; Pang and Guo 2017; Miehe et al. 2019). Therefore, the clonal growth of the tussock-forming *K. pygmaea* and the rhizomatous *K. humilis* drives their population recruitment, and further shapes plant community succession in the alpine meadows where they dominate. Understanding the effect of disturbance by plateau pikas on the clonal growth of the tussock-forming *K. pygmaea* and the rhizomatous *K. humilis* is vital to partially explain the variation in plant community with the presence of plateau pikas. The clonal growth performance of the tussock-forming *K. pygmaea* and the rhizomatous *K. humilis* populations under disturbance by plateau pikas is often determined by studying clonal traits and bud bank traits. The aim of this study was to investigate the effects of disturbance by plateau pikas on clonal traits and bud bank traits in the tussock-forming *K. pygmaea* and the rhizomatous *K. humilis*. This study hypothesized that perennial graminoids in the plant community affected by small herbivore activities will respond by (1) increasing the number of shoots and the production of rhizomes; (2) decreasing spacer length and increasing spacer number; and (3) increasing the number of buds in the bud bank (on shoot bases and along rhizomes and entire clonal fragments).

Materials and methods

Study area description

Since plateau pikas can live in a vast area that includes variations in soil types, topography and microclimates on the Qinghai-Tibetan Plateau, this study selected three sites in Gansu Province as survey sites where plateau pikas are present to identify a general pattern of the clonal growth of the tussock-forming *K. pygmaea* and the rhizomatous *K. humilis* in relation to the presence of plateau pikas across different environments. These survey sites are located at Azi Cattle station in Maqu County and Gaxiu town and Gahai town in Luqu County (Table 1) and experience the same cold, humid plateau continental climate. Although elevations, precipitations and temperatures are different among three survey sites, the precipitation can form natural gradient. This study classified the three survey sites as relative low precipitation site (Azi), intermedium precipitation site (Gaxiu) and relative high precipitation site (Gahai). At the survey three sites, alpine meadows account for 80% of the total land area. These alpine meadows are dominated by tussock-forming *K.*

Table 1 Description of the study areas at Azi, Gaxiu and Gahai

Site	Longitude	Latitude	Elevation(m)	MAT(℃)	MAP(mm)	Dominant species	Main associate species
Azi	100°40′-102°29′ E	33°06′-34°30′ N	3530	-3.0 ~ 3.0	564 (Relative low)	*Kobresia pygmaea*	*Elymus nutans* *K. humilis* *Leontopodium japonicum*
Gaxiu	101°35′-102°58′ E	33°58′-34°48′ N	3505	1.0–3.0	633 (Intermedium)	*K.pygmaea*	*Agropyron cristatum* *E. nutans* *K. humilis*
Gahai	102°08′-102°47′ E	33°97′-34°32′ N	3110	1.2	781 (Relative high)	*K. humilis*	*K.pygmaea* *Poa pratensis* *L. japonicum*

MAT is the mean annual temperature; MAP is the mean annual precipitation

pygmaea in Azi and Gaxiu and are dominated by rhizomatous *K. humilis* in Gahai. These alpine meadows are often fenced to prevent yak and Tibetan sheep grazing from mid-April to early October, and the fences are opened to graze yak and Tibetan sheep from mid-October to early April, with 3.4 yak^{-1} grazing stock rates.

Plateau pikas are the only small herbivores that appeared in the alpine meadows at each survey site. The plateau pika population peaks in August (Dobson et al. 1998) and plateau pikas mostly disturb alpine meadows.

Experimental design

Plateau pikas often live in group, and prefer open-vegetation habitats (Fan et al. 1999; Zhang et al. 2020). Since most plateau pikas are philopatric (Dobson et al. 1998), they usually live in territorial and patchy patterns on alpine meadows (Zhang et al. 2020; Pang et al. 2020). Some alpine meadows without plateau pikas are potentially suitable habitats for this small burrowing herbivore. Plateau pikas can gradually spread from their current suitable habitats to other suitable habitats. Therefore, sites showing an absence of plateau pikas can easily be found.

This study used a random stratified and paired design to select the plots at each site. At each site, ten disturbed plots where plateau pikas were present and where active burrow entrances were observed in the field were selected. The distance between two disturbed plots was approximately 5 km. Next, a paired adjacent undisturbed plot for each disturbed plot was selected in alpine meadows where the plateau pika was absent. The disturbed and undisturbed plots were 500 m to 1 km apart to ensure that the undisturbed plot was a true reference plot. If the distance between the disturbed plot and its paired undisturbed plot were too small, there would be overlap between the disturbed and undisturbed plots (Pang et al. 2020). If the distance between the disturbed plot and its paired undisturbed plot were too far, it would be difficult to ensure the same alpine meadow conditions and microclimates between paired plots. The size of each plot was 35 m × 35 m, approximately, the home range of plateau pikas with an area of 1262.5 m^2 (Fan et al. 1999). This plot design ensured that each set of paired plots was part of the same alpine meadow and had similar plant composition, topography and climate conditions. Each paired plot was managed with the same practices. In total, there were 10 paired plots at each site and 60 plots across the three sites, including 30 disturbed plots and 30 undisturbed plots.

Plateau pikas often select plants to consume throughout their home range (Jiang 1985; Fan et al. 1999). In addition, plateau pika can create many bare soil patches in their home range, which manifests as a discrete mosaic of vegetated land and bare land over a range of spatial scales (Yu et al. 2017; Smith et al. 2019). The areas of these bare soil patches were different and dependent on the pika population (Sun et al. 2015; Liu et al. 2017; Pang et al. 2019). Although the areas of bare soil were different among the plots, this study selected 30 disturbed plots with different bare soil areas in each plot, on a large scale, which facilitated the discovery of a general pattern about the effects of disturbance by plateau pikas on the clonal growth of the two graminoids. All plots were established in alpine meadows that were fenced from mid-April to early October and were grazed by yak and Tibetan sheep from mid-October to early April.

Sampling

Clonal plants often consist of many single shoots and rhizomes; the shoots are connected by rhizomes that originate from a single primary shoot (Ganie et al. 2016). The connective length between two consecutive shoots along a rhizome is called the spacer length (Ye et al. 2006). These numerous tillers and rhizomes constitute a completely clonal unit, called the entire clonal fragment. Based on common indicators of clonal traits (Wang et al. 2004; Ye et al. 2006; Gough et al. 2012; Ganie et al. 2016) and bud bank traits (VanderWeide and Hartnett 2015) developed in previous studies, this study used the ramet number per clonal fragment, the rhizome length per clonal fragment, the rhizome branch number per clonal fragment, the spacer length and the spacer number per clonal fragment to estimate the clonal traits, and used the bud type, placement, and number to evaluate the bud bank traits.

In each disturbed and undisturbed plot, 20 *K. pygmaea* clonal fragments and 20 *K. humilis* clonal fragments that were fully developed were randomly chosen, and all rhizomes and shoots for each clonal fragment of the selected plant were sampled. First, the target plants were randomly selected and labeled in each plot. Second, a sketch of the plant clonal fragments with complete shoots was created for each target plant. For each target plant, the soil adjacent to the plant was gently removed to expose the main rhizome. Along each rhizome, the top layer of soil was also gently removed to ensure that the whole rhizome and the shoots were exposed as completely as possible; care was taken to ensure that the rhizome and the shoots were not damaged. Third, based on the sketch of each target plant, the entire clonal fragment of each target plant was sampled. Fourth, each plant with the entire clonal fragment was immediately placed in a sealable plastic bag and stored at 4 °C until further processing. In total, this study sampled 1200 clonal fragments from each plant species, consisting of 600 clonal fragments from the disturbed plots and 600 clonal fragments from the undisturbed plots. In the laboratory, the rhizome branch number and the spacer number of each clonal fragment were recorded. The shoot number per each rhizome branch was recorded. The shoot number for each clonal fragment was the sum of the shoot numbers for all rhizome branches of that clonal fragment. A ruler was used to measure the spacer length and the rhizome length of each clonal fragment, and the average value of all spacer lengths was considered the spacer length for that clonal fragment. Finally, a dissecting microscope was used to record the tiller bud number per shoot and the rhizome bud number per rhizome branch. The tiller bud number per clonal fragment was the sum of the tiller bud numbers of all shoots from that clonal fragment. The rhizome bud number per clonal fragment was the sum of the rhizome bud numbers for all rhizome branches of that clonal fragment.

Statistical analysis

The values for each parameter for all clonal fragments within each plot were pooled. First, a two-way analysis of variance (ANOVA) with the general linear model (GLM) was used to analyze the effects of plateau pika disturbances, the effect of site and their interactions on the shoot number, rhizome branch number, rhizome length, spacer number, spacer length per clonal fragment, tiller bud number per shoot, rhizome bud number per rhizome branch, tiller bud number and rhizome bud number per clonal fragment of *K. pygmaea* or *K. humilis* to develop a general pattern of clonal traits and bud bank traits in relation to the disturbance by plateau pika. In the model, the abovementioned parameters acted as response variables, and the disturbance by plateau pika (Dist.), the site (Site) and their interactions were introduced as predictors.

Second, since the clonal fragment samples of each species from the disturbed and undisturbed plots were paired and generally were not normally distributed, the nonparametric Wilcoxon–Mann–Whitney test was used to evaluate the effects of disturbance by plateau pikas on the shoot number, rhizome branch number, rhizome length, spacer length, spacer number per clonal fragment, tiller bud number per shoot, rhizome bud number per rhizome branch, tiller bud number and rhizome bud number per clonal fragment of *K. pygmaea* or *K. humilis* at each site in order to support the general pattern.

All statistical analyses were performed with R Version 3.2.2, R Foundation for Statistical Computing, Vienna, Austria.

Results

Effects of disturbance by plateau pikas on clonal traits of *K. pygmaea* and *K. humilis*

The disturbance by plateau pika (Dist.) and the three sites (Site) had significant impacts on the shoot number, the rhizome branch number, the rhizome length and the spacer number per clonal fragment of *K. pygmaea* and *K. humilis* and on the spacer lengths per clonal fragment of *K. humilis* (Table 2). The interaction of Dist. and Site had significant impacts on the rhizome length and rhizome branch number per clonal fragment of *K. pygmaea* and *K. humilis,* on the spacer length per clonal fragment of *K. pygmaea,* and on the spacer number per clonal fragment of *K. humilis*, whereas this interaction had no impact on the shoot number per clonal fragment of *K. pygmaea* and *K. humilis*, on the spacer number per clonal fragment of *K. pygmaea,* or on the spacer length per clonal fragment of *K. humilis*.

When the data from three sites were analyzed together, disturbance by plateau pikas increased the shoot number, rhizome branch number, rhizome length and spacer number per clonal fragment of *K. pygmaea* and *K. humilis* and increased the spacer length per clonal fragment of *K. humilis* (Fig. 1).

When the data from each site were analyzed separately, the responses of the shoot number per clonal fragment to disturbance by plateau pikas were similar between *K. pygmaea* and *K. humilis* and among the three sites (Figs. 2, 3). However, the response of the rhizome branch number per clonal fragment to disturbance by plateau pikas was different between *K. pygmaea* and *K. humilis* and among the

Table 2 Shoot number per clonal fragment, rhizome branch number per clonal fragment, spacer length and spacer number of *K. pygmaea* and *K. humilis* in the relationship to the disturbance by plateau pikas (Dist.), the sites (Site) and their interaction based on general linear models

Response variable		Site		Dist		Site × Dist	
		F	*P*	F	*P*	F	*P*
Kobresia pygmaea	Shoot number per clonal fragment	46.830	**0.000**	54.567	**0.000**	0.301	0.860
	Rhizome branch number per clonal fragment	39.967	**0.000**	44.704	**0.000**	22.403	**0.000**
	Rhizome length	14.950	**0.000**	8.216	**0.004**	7.138	**0.028**
	Spacer length	12.966	**0.002**	2.267	0.132	9.456	**0.009**
	Spacer number	46.830	**0.000**	54.567	**0.000**	0.301	0.860
K. humilis	Shoot number per individual	309.414	**0.000**	45.593	**0.000**	0.311	0.856
	Rhizome branch number per clonal fragment	11.494	**0.003**	38.082	**0.000**	1.803	0.406
	Rhizome length	49.270	**0.000**	66.015	**0.000**	11.967	**0.003**
	Spacer length	54.978	**0.000**	20.523	**0.000**	7.349	**0.025**
	Spacer number	309.414	**0.000**	45.593	**0.000**	0.311	0.856

The shoot number per clonal fragment, rhizome branch number per clonal fragment, rhizome length per clonal fragment, spacer number per clonal fragment and spacer length act as response variables, while the predictors were: whether an area was disturbed by plateau pikas (Dist.), the three survey sites (Site), and their interaction. Significant *P* values (< 0.05) are in bold

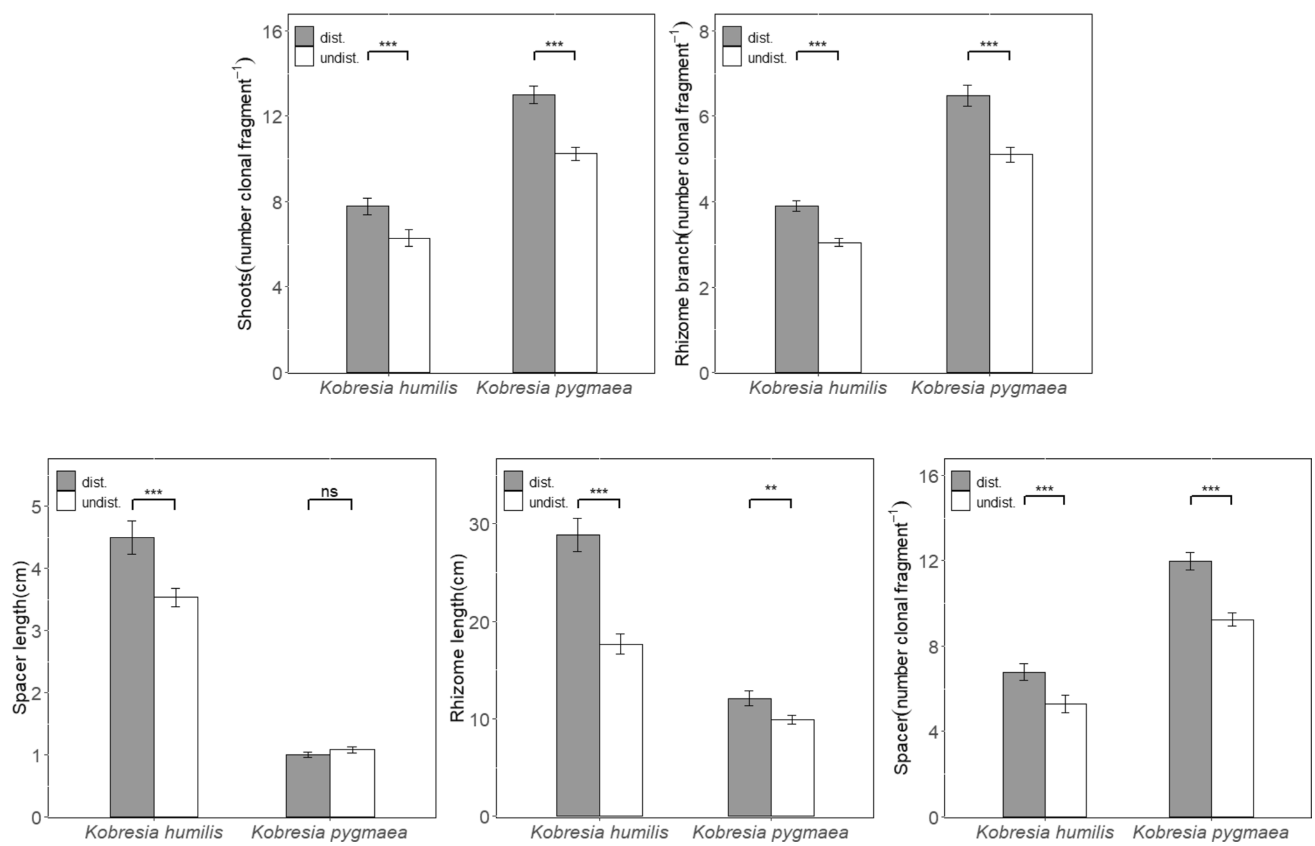

Fig. 1 Shoot number, rhizome branch number, rhizome length, spacer length and spacer number per clonal fragment of *K. pygmaea* and *K. humilis* in the presence of disturbance and in the absence of disturbance by plateau pika. The error bars represent the standard errors. *Significant differences at $P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, ns $P > 0.05$

three sites. The disturbance by plateau pikas increased the rhizome branch number per clonal fragment of *K. pygmaea* and *K. humilis* in relative low precipitation site (Azi) and intermediate precipitation site (Gaxiu) and increased the rhizome branch number per clonal fragment of *K. humilis* in relative high precipitation site (Gahai), whereas disturbance

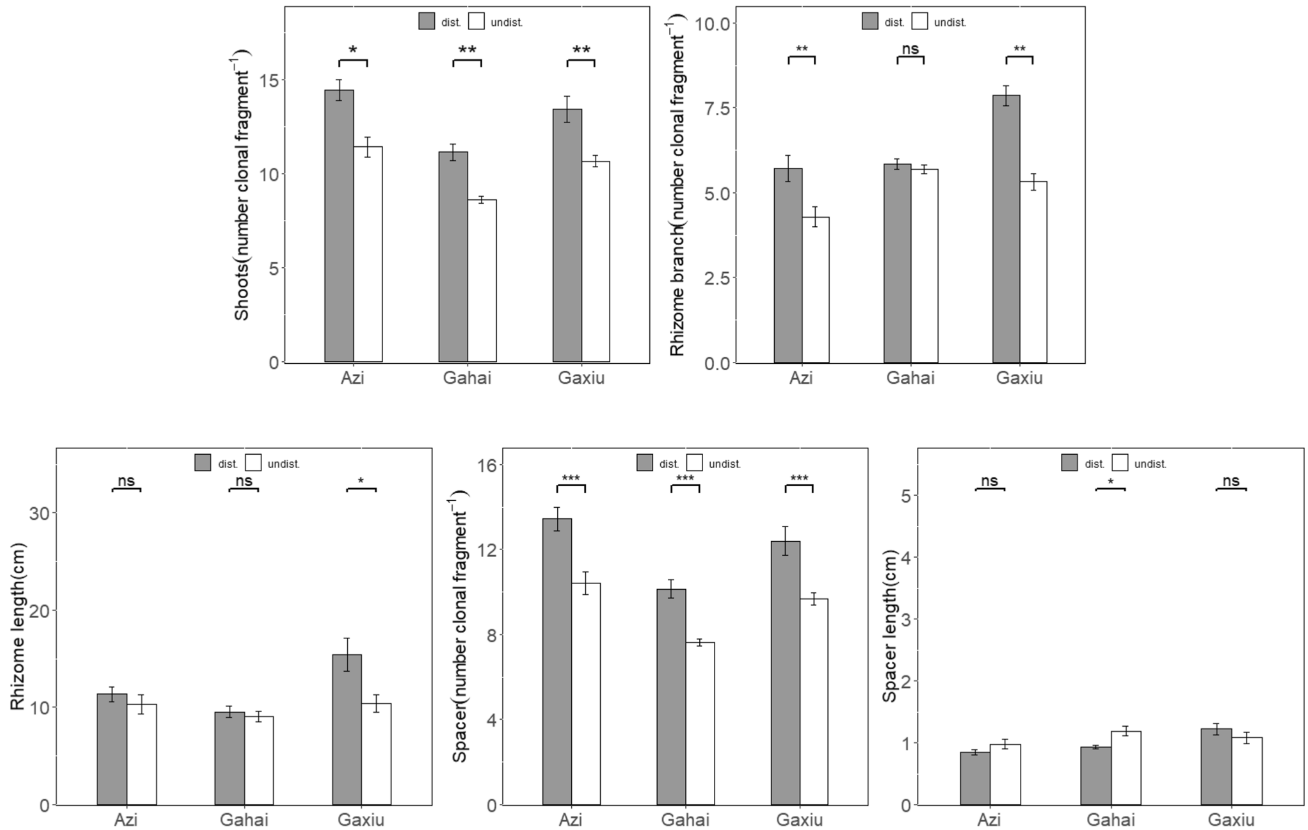

Fig. 2 Shoot number, rhizome branch number, rhizome length, spacer length and spacer number per clonal fragment of *K. pygmaea* in the presence of disturbance and in the absence of disturbance by plateau pika at Azi, Gahai and Gaxiu. The error bars represent the standard errors. *Significant differences at $P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ns $P > 0.05$

by plateau pikas had no impact on the clonal fragments of *K. pygmaea* in relative high precipitation site. The effects of plateau pikas disturbances on the rhizome length were different among the three sites, and between *K. pygmaea* and *K. humilis*. The disturbance by plateau pika increased the rhizome length of *K. humilis* in relative low precipitation site, intermediate precipitation site and relative high precipitation site, and *K. pygmaea* in relative high precipitation site, whereas it had no impact on the rhizome length of *K. pygmaea* in relative low precipitation site and higher precipitation site. The responses of the spacer number to disturbance by plateau pikas were different between *K. pygmaea* and *K. humilis,* and among the three sites. The responses of the spacer number to plateau pika disturbances were similar between *K. pygmaea* and *K. humilis* and among the three sites. The disturbance by plateau pikas had different impacts on the spacer length per clonal fragment among the three sites and between *K. pygmaea* and *K. humilis*. The spacer length per clonal fragment of *K. pygmaea* was lower in the disturbed plots than in the undisturbed plots in relative high precipitation site, whereas it was not significantly different between the disturbed plots and the undisturbed plots in relative low precipitation site and intermediate precipitation site. For clonal fragments of *K. humilis,* plateau pika disturbance significantly increased the spacer length in relative low precipitation site and intermediate precipitation site, but had no effect on this parameter in relative high precipitation site.

Effects of disturbance by plateau pikas on bud bank traits of *K. pygmaea* and *K. humilis*

The disturbance by plateau pika (Dist.) showed significant influence on the tiller bud number per shoot, the tiller bud number per clonal fragment, the rhizome bud number per clonal fragment of *K. pygmaea* and *K. humilis,* and the rhizome bud number per rhizome branch of *K. pygmaea* and *K. humilis* (Table 3). The three sites (Site) showed significant impacts on the tiller bud number per shoot, the rhizome bud number per rhizome branch, the tiller bud number per clonal fragment, and the rhizome bud number per clonal fragment of *K. pygmaea* and *K. humilis.* The interaction of Dist. and Site showed significant impacts on the rhizome bud number per clonal fragment of *K. pygmaea* and on the tiller bud number per shoot and the tiller bud number per clonal fragment of *K. humilis*, whereas it had no impact on the tiller bud number per shoot, the rhizome bud number per rhizome

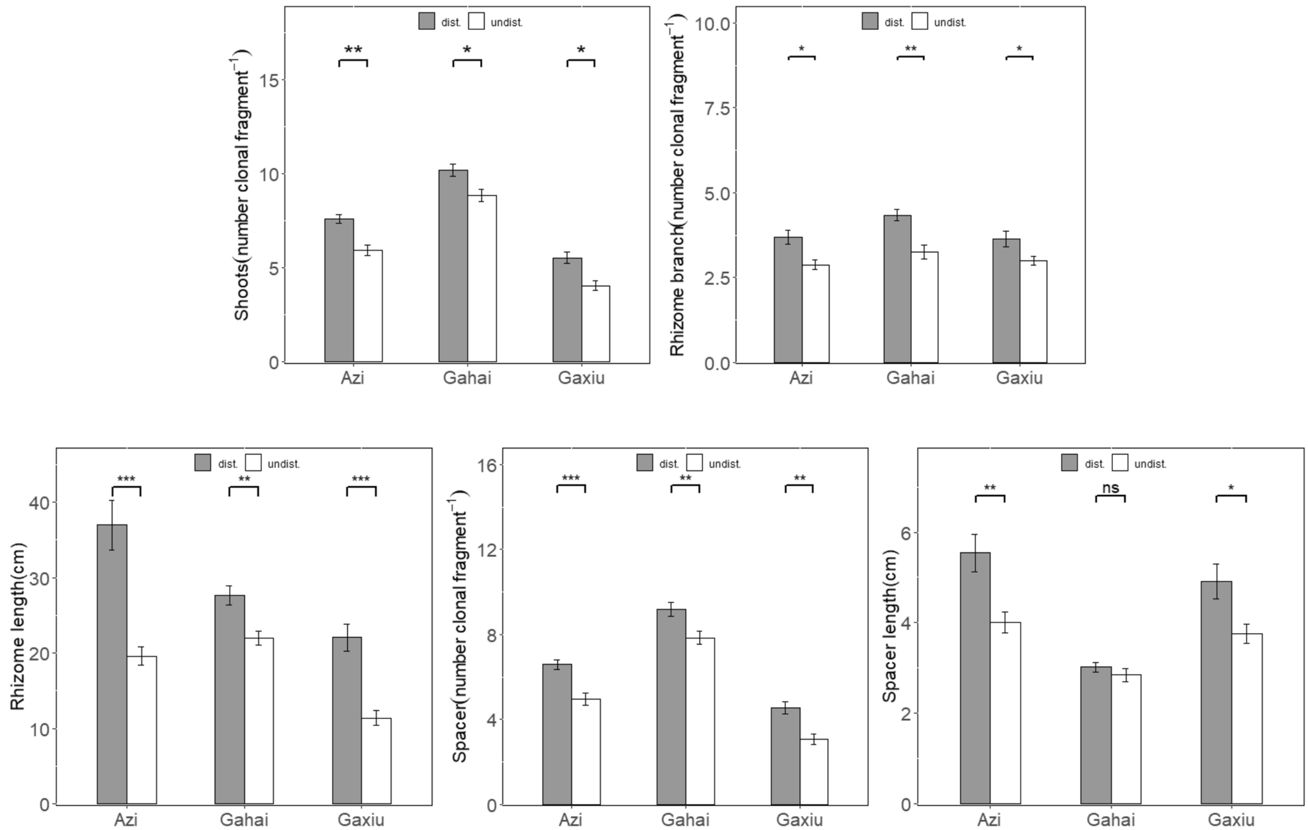

Fig. 3 Shoot number, rhizome branch number, rhizome length, spacer length and spacer number per clonal fragment of *K. humilis* in the presence of disturbance and in the absence of disturbance by plateau pika at Azi, Gahai and Gaxiu. The error bars represent the standard errors. *Significant differences at $P<0.05$, **$P<0.01$, ***$P<0.001$, ns $P>0.05$

Table 3 Tiller bud number per shoot, rhizome bud number per rhizome branch, tiller bud number per clonal fragment and rhizome bud number per clonal fragment of *K. pygmaea* and *K. humilis* in relation to the disturbance of plateau pikas (Dist.), the site (Site) and their interaction based on general linear models

Response variable		Site		Dist		Site × Dist	
		F	*P*	F	*P*	F	*P*
K.pygmaea	Tiller bud number per shoot	108.799	**0.000**	5.048	**0.025**	2.310	0.315
	Rhizome bud number per rhizome branch	42.486	**0.000**	0.191	**0.662**	0.449	0.799
	Tiller bud number per clonal fragment	237.00	**0.000**	61.771	**0.000**	0.075	0.963
	Rhizome bud number per clonal fragment	35.635	**0.000**	12.897	**0.000**	6.536	**0.038**
K. humilis	Tiller bud number per shoot	11.574	**0.003**	21.653	**0.000**	12.893	**0.002**
	Rhizome bud number per rhizome branch	37.834	**0.000**	10.789	**0.001**	0.438	0.803
	Tiller bud number per clonal fragment	59.998	**0.000**	73.292	**0.000**	7.394	**0.025**
	Rhizome bud number per clonal fragment	30.336	**0.000**	57.317	**0.000**	6.213	0.045

The tiller bud number per shoot, rhizome bud number per rhizome branch, tiller bud number per clonal fragment and rhizome bud number per clonal fragment act as response variables while the predictors were: whether an area was the disturbed by plateau pikas (Dist.), the three survey sites (Site), and their interaction. Significant *P* values (<0.05) are in bold

branch, and the tiller bud number per clonal fragment of *K. pygmaea*, or on the rhizome bud number per clonal fragment of *K. humilis*.

When the data from three sites were analyzed together, the plateau pika disturbances increased the tiller bud number, the rhizome bud number per clonal fragment of *K. pygmaea* and *K. humilis*, and the tiller bud number per shoot and the rhizome bud number per rhizome branch of *K. humilis* (Fig. 4).

When the data from each site were analyzed separately, the effects of plateau pika disturbances on the tiller bud number per shoot were different among the three sites, and

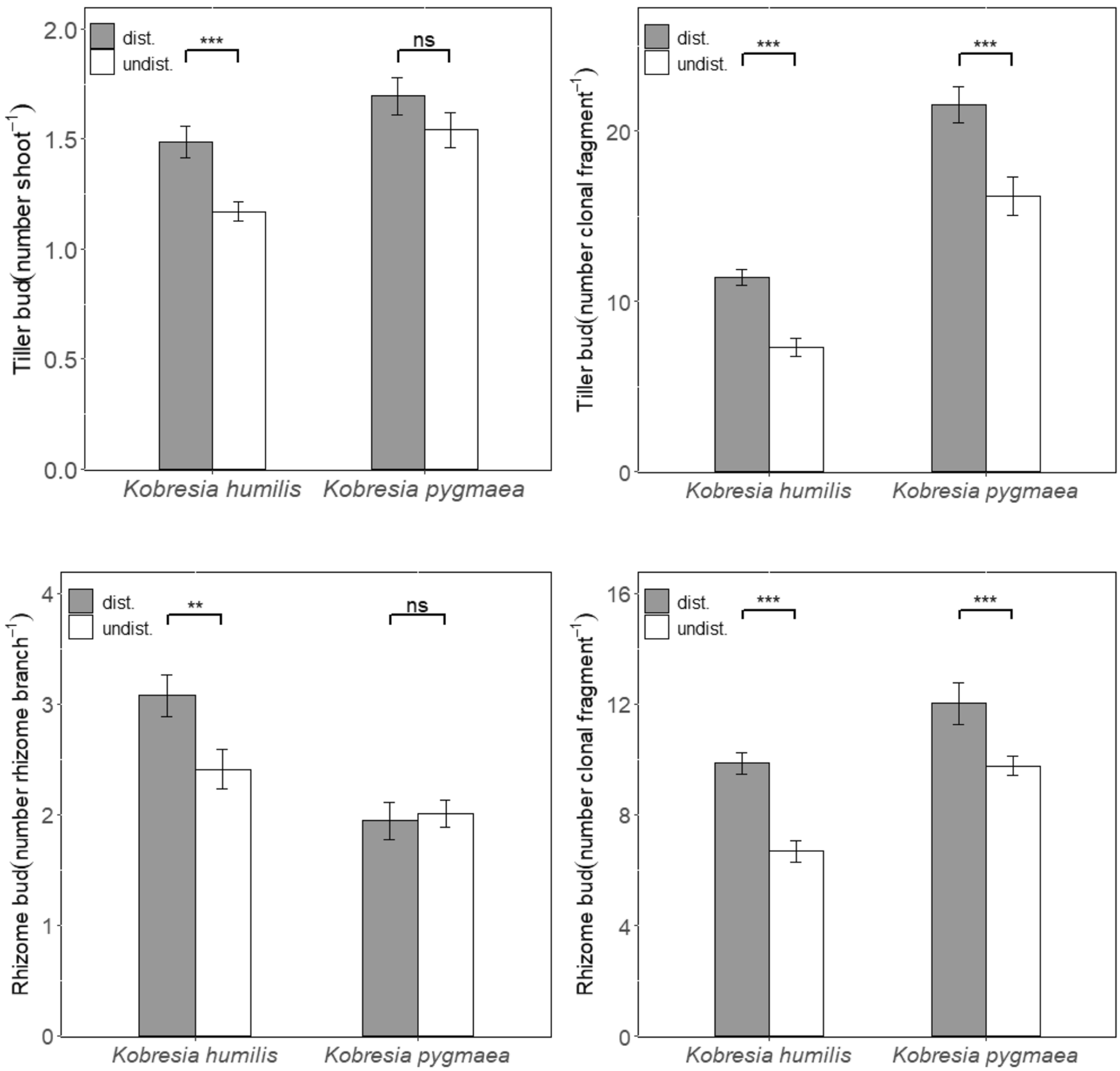

Fig. 4 Tiller bud number per shoot, the rhizome bud number per rhizome branch, tiller bud number per clonal fragment and the rhizome bud number per clonal fragment of *K. pygmaea* and *K. humilis* in the presence of disturbance and in the absence of disturbance by plateau pika. The error bars represent the standard errors. *Significant differences at $P<0.05$, **$P<0.01$, ***$P<0.001$, ns $P>0.05$

between *K. pygmaea* and *K. humilis* (Figs. 5, 6). The disturbance by plateau pikas increased the tiller bud density per shoot of *K. humilis* in relative low precipitation site (Azi) and intermediate precipitation site (Gaxiu) and of *K. pygmaea* in relative high precipitation site (Gahai), whereas it had no impact on the tiller bud density per shoot of *K. pygmaea* in relative low precipitation site and intermediate precipitation site, or that of *K. humilis* in relative high precipitation site. The effects of plateau pika disturbances on the tiller bud number per clonal fragment were similar among the three sites, and between *K. pygmaea* and *K. humilis*. The responses of the rhizome bud density per rhizome branch to disturbance by plateau pikas were different between *K. pygmaea* and *K. humilis* and among the three sites. The disturbance by plateau pikas increased the rhizome bud density per rhizome branch of *K. humilis* in relative low precipitation site and intermediate precipitation site, whereas it had no effect on the rhizome bud density per rhizome branch of *K. pygmaea* in relative low precipitation site, intermediate precipitation site or relative high precipitation site, or on that of *K. humilis* in relative high precipitation site. The responses of the rhizome bud number per clonal fragment to plateau pika disturbances were different between *K. pygmaea* and *K. humilis* and among the three sites. Plateau pika disturbances increased the rhizome bud number per clonal fragment of *K. pygmaea* in relative low precipitation site and intermedium precipitation site and per clonal fragment of *K. humilis* in relative low precipitation site, intermediate precipitation site and relative high precipitation site, whereas plateau pika disturbance had no effect on the rhizome bud

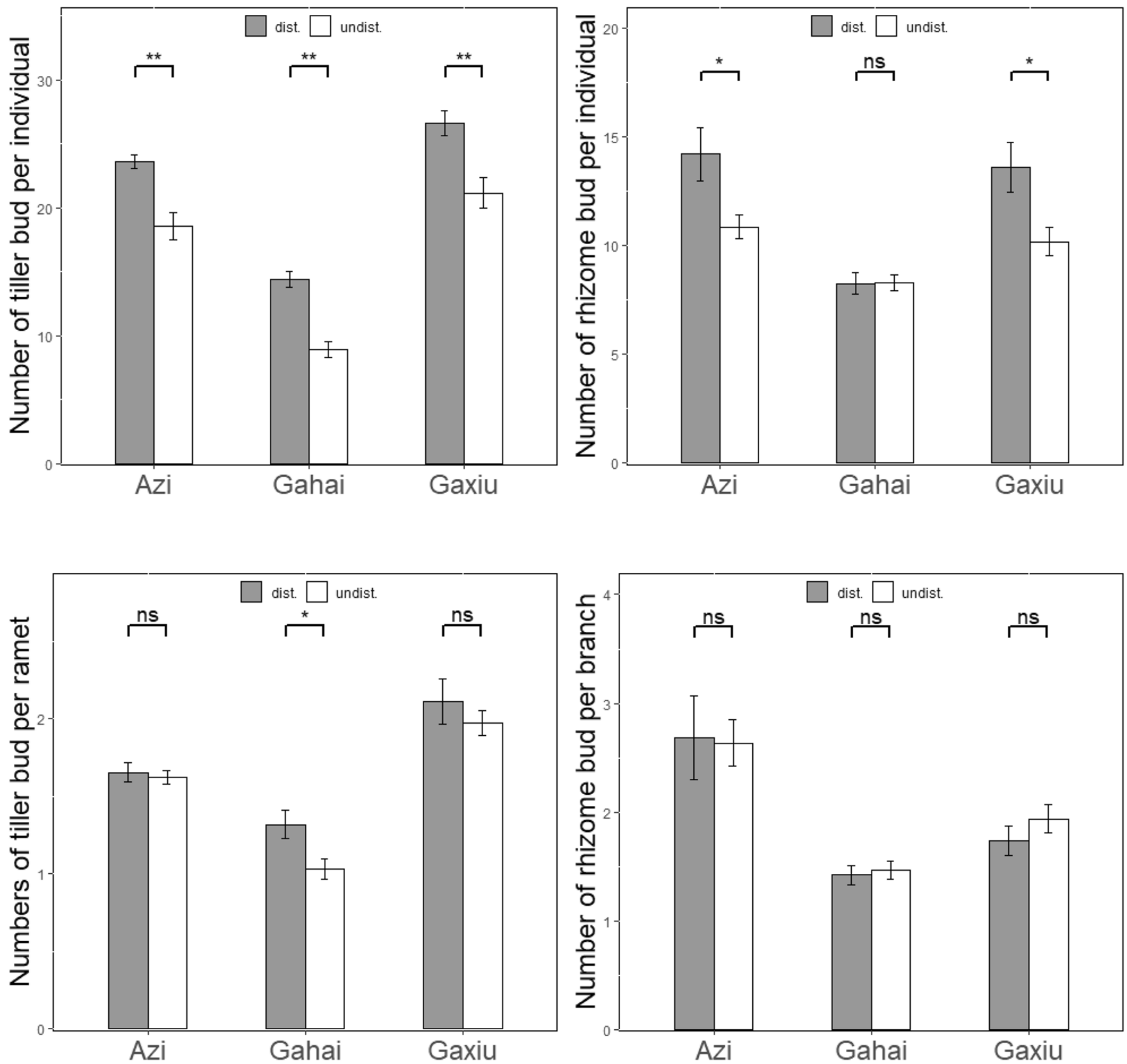

Fig. 5 Tiller bud number per shoot, the rhizome bud number per rhizome branch, tiller bud number per clonal fragment and the rhizome bud number per clonal fragment of *K. pygmaea* in the presence of disturbance and in the absence of disturbance by plateau pika at Azi, Gahai and Gaxiu. The error bars represent the standard errors. *Significant differences at $P<0.05$, **$P<0.01$, ***$P<0.001$, ns $P>0.05$

number per clonal fragment of *K. pygmaea* in relative high precipitation site.

Discussion

This study finds that disturbance by plateau pikas increased the shoot number, rhizome branch number and rhizome length of *K. pygmaea* and *K. humilis* across three sites, similar to the first hypothesis; these results have also been reported for large-herbivore grazing (Jonsdottir 1991; Jinhua et al. 2010). The increases in shoots and rhizome branches and longer rhizome per clonal fragment in the presence of plateau pikas can be caused by two mechanisms. First, consumption by plateau pikas eliminates apical dominance (Wang et al. 2018) or stimulating plant compensatory growth (Mcnaughton 1983) in the two plants, encouraging the lateral buds to produce more shoots (Hendrickson and Briske 1997; Wang et al. 2004) and producing more rhizome branch and longer rhizome. Second, the higher soil nutrient concentrations caused by plateau pika disturbances (Yu et al. 2017) are beneficial for the two plants producing more shoots and rhizome branches and longer rhizomes (Gough et al. 2012). However, this study shows that the response of rhizome branch number per clonal fragment in tussock-forming *K. pygmaea* to plateau pika disturbances is site dependent. These results suggest that disturbance by plateau pikas is beneficial for the current population recruitment of the tussock-forming *K. pygmaea* and the rhizomatous *K. humilis* in a plant community.

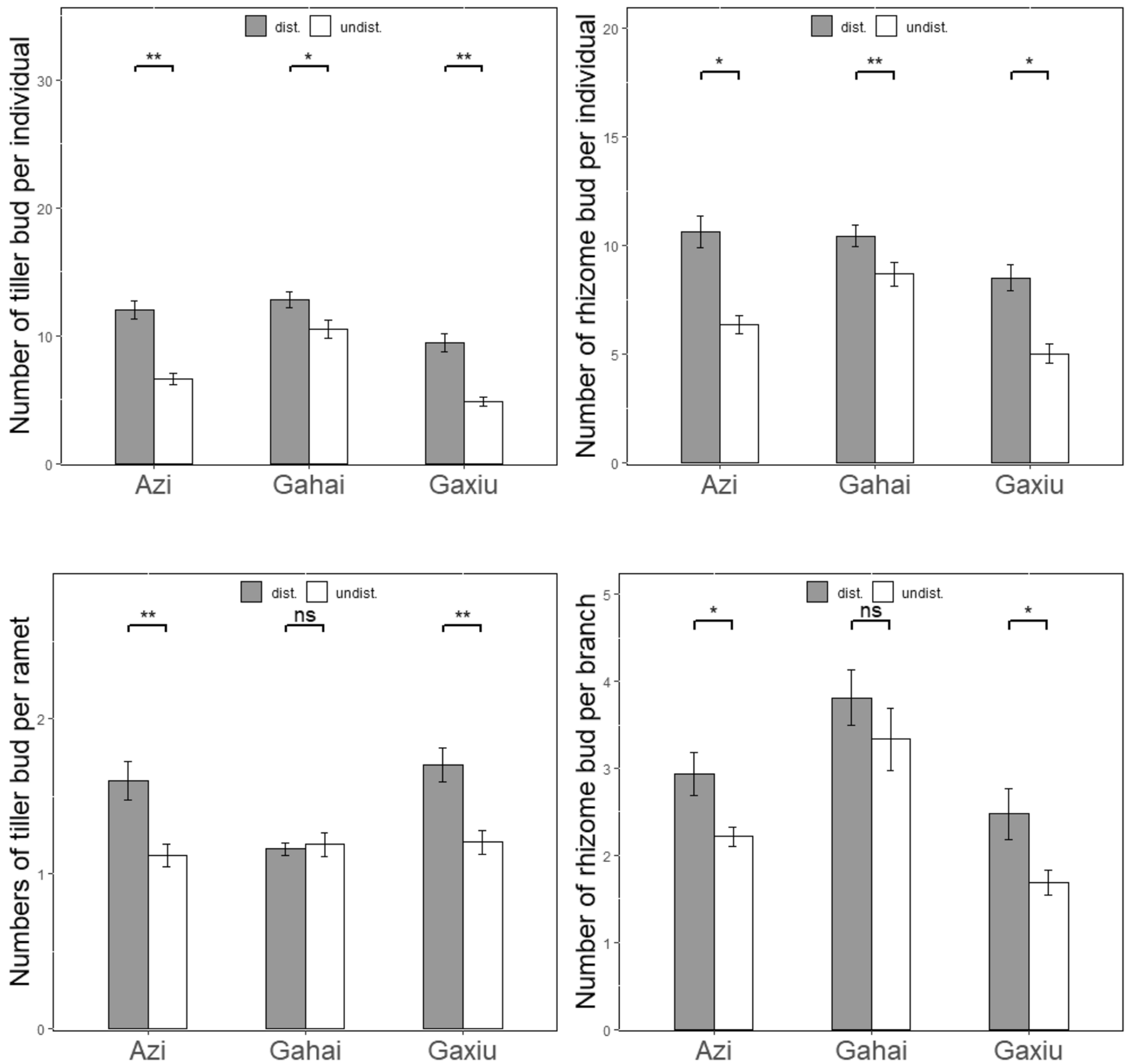

Fig. 6 Tiller bud number per shoot, the rhizome bud number per rhizome branch, tiller bud number per clonal fragment and the rhizome bud number per clonal fragment of *K. humilis* in the presence of disturbance and in the absence of disturbance by plateau pika at Azi, Gahai and Gaxiu. The error bars represent the standard errors. *Significant differences at $P<0.05$, **$P<0.01$, ***$P<0.001$, ns $P>0.05$

Disturbance by plateau pikas increased the spacer number of the tussock-forming *K. pygmaea* and the rhizomatous *K. humilis* and the spacer length of the rhizomatous *K. humilis*, whereas it had no impact on the spacer length of the tussock-forming *K. pygmaea*, which is not consistent with the second hypothesis. Previous studies have shown that large-herbivore grazing often decreases spacer lengths (Jinhua et al. 2010; Johansen et al. 2016). Trampling by livestock often damages the shoot connections along the rhizomes (Benot et al. 2011a), which can divide one clonal fragment into many smaller clonal fragments, resulting in a decrease in spacer length per clonal fragment for those plants (Benot et al. 2011b). Trampling by plateau pikas is too slight to affect the shoot connections because of the low weight of the plateau pikas (approximately 150 g) (Pang et al. 2019). In this case, rhizomatous *K. humilis* usually adapts to a heterogeneous habitat by extending its spacer lengths to expand its population by producing other new shoots (Humphrey and Pyke 1998; Ye et al. 2015). However, the tussock-forming *K. pygmaea* generally adapts to a heterogeneous habitat by rapidly producing more new tillers on its tussock shoots (Doust 1981; Ye et al. 2006; Herben et al. 2015; Zheng et al. 2019) rather than by changing the spacer length for each clonal fragment. Consequently, the responses of the spacer lengths to disturbance by plateau pikas are different between the tussock-forming *K. pygmarea* and the rhizomatous *K. humilis*.

This study also finds that disturbance by plateau pikas increases the tiller bud number and the rhizome bud number for clonal fragments of the tussock-forming *K. pygmaea* and the rhizomatous *K. humilis* as well as the tiller bud number per shoot and the rhizome bud number per rhizome branch of rhizomatous *K. humilis*, whereas disturbance had no impact on the tiller bud number per shoot or the rhizome bud number per rhizome branch of the tussock-forming *K. pygmaea,* this finding is not consistent with the third hypothesis. There are two related explanations for how disturbance by plateau pikas increases the tiller bud number and the rhizome bud number for clonal fragments of the tussock-forming *K. pygmaea* and the rhizomatous *K. humilis*: first, the higher shoot number and rhizome branch number per clonal fragment in the presence of plateau pikas can increase the tiller bud number and the rhizome bud number for each clonal fragment; second, consumption by plateau pikas can stimulate the two plant species to produce more tiller buds on one shoot to recruit the aboveground population of clonal fragments (Jiang 1985; Wang et al. 2018). There are additional, different explanations for how plateau pika disturbance increases the tiller bud number and the rhizome bud number for clonal fragments of the tussock-forming *K. pygmaea* and the rhizomatous *K. humilis,* in which disturbance by plateau pikas has different impacts on the tiller bud number per shoot and the rhizome bud number per rhizome branch between the tussock-forming *K. pygmaea* and the rhizomatous *K. humilis*. Tussock-forming *K. pygmaea* often uses most of its tiller buds on each shoot to produce new tussock shoots to monopolize the spatially heterogeneous habitat (Zheng et al. 2019) caused by plateau pika disturbances, whereas rhizomatous *K. humilis* produces new spreading shoots from the rhizome to escape the heterogeneous habitat (Ye et al. 2015) caused by plateau pikas (Yu et al. 2017) and to utilize soil nutrients at a larger scale (Pottier and Evette 2010), with little reduction in the number of tiller buds on each shoot. Consequently, an increase in the tiller bud number per shoot for *K. pygmaea* was not observed, whereas the greatest increase in the tiller bud number per shoot was observed in rhizomatous *K. humilis*. In addition, the tussock-forming *K. pygmaea* may prefer to strengthen its rhizome branch in the heterogeneous habitat (Rusch et al. 2010) caused by plateau pika disturbances and maintain the denser rhizome architecture rather than producing rhizome buds, whereas rhizomatous *K. humilis* often produces as many rhizome buds as possible to produce more spreading shoots in heterogeneous habitat (Wang et al. 2018) induced by plateau pika disturbances. The higher tiller bud numbers and rhizome bud numbers per clonal fragment caused by plateau pikas indicate that the presence of plateau pikas can improve the potential population recruitment of both the tussock-forming *K. pygmaea* and the rhizomatous *K. humilis* in the long term.

Conclusions

This study employed plateau pikas to investigate the responses of clonal traits and bud bank traits of graminoids to disturbances by small burrowing herbivores. This study shows a general pattern in which plateau pika disturbance increases the shoot number, spacer number and tiller bud number for clonal fragments of *K. pygmaea* and *K. humilis*. Although plateau pika disturbances increase the rhizome branch number, the rhizome length and the rhizome bud number for clonal fragments of *K. pygmaea* and *K. humilis*, as well as the spacer lengths, the tiller bud number per shoot, and the rhizome bud number per rhizome branch of *K. humilis*, there was no impact on the spacer length, the tiller bud number per shoot, or the rhizome bud number per rhizome branch of *K. pygmaea* across the three sites; the effects of plateau pika disturbances on spacer length, rhizome branch number and rhizome bud number per clonal fragment are not only dependent on the clonal growth form of the plant but are also related to the dominance degree of one species. The findings from this study present a possible hypothesis for how perennial plants with different clonal growth forms adapt to the disturbed habitats induced by plateau pikas and how disturbances by a small burrowing herbivore contribute to population regeneration in perennial plants with different clonal growth forms.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The *Kobresia pygmaea* and *K. humilis* are not endangered and endemic species.

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