

Response of *Polygonum viviparum* Species and Community Level to Long-term Livestock Grazing in Alpine Shrub Meadow in Qinghai-Tibet Plateau

Zhi-Hong Zhu^{1*}, Jeremy Lundholm², Yingnian Li³ and Xiaoan Wang¹

¹College of Life Sciences, Shaanxi Normal University, Xi'an 710062, China;

²Biology Department/Environmental Studies Program, Saint Mary's University, Halifax, Nova Scotia, Canada, B3H 3C3;

³Northwest Institute of Plateau Biology, the Chinese Academy of Sciences, Xining 810008, China)

Abstract

Grazing by domestic herbivores is generally recognized as a major ecological factor and an important evolutionary force in grasslands. Grazing has both extensive and profound effects on individual plants and communities. We investigated the response patterns of *Polygonum viviparum* species and the species diversity of an alpine shrub meadow in response to long-term livestock grazing by a field manipulative experiment controlling livestock numbers on the Qinghai-Tibet Plateau in China. Here, we hypothesize that within a range of grazing pressure, grazing can alter relative allocation to different plant parts without changing total biomass for some plant species if there is life history trade-offs between plant traits. The same type of communities exposed to different grazing pressures may only alter relative species' abundances or species composition and not vary species diversity because plant species differ in resistant capability to herbivory. The results show that plant height and biomass of different organs differed among grazing treatments but total biomass remained constant. Biomass allocation and absolute investments to both reproduction and growth decreased and to belowground storage increased with increased grazing pressure, indicating the increasing in storage function was attained at a cost of reducing reproduction of bulbils and represented an optimal allocation and an adaptive response of the species to long-term aboveground damage. Moreover, our results showed multiform response types for either species groups or single species along the gradient of grazing intensity. Heavy grazing caused a 13.2% increase in species richness. There was difference in species composition of about 18%–20% among grazing treatment. Shannon-Wiener (H') diversity index and species evenness (E) index did not differ among grazing treatments. These results support our hypothesis.

Key words: alpine shrub meadow; biomass allocation; grazing response; relative species' abundances; species diversity.

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Grazing by large herbivores is generally recognized as a major ecological factor and an important evolutionary force in grasslands (Harper 1977). After repeated exposure to intensive defoliation, plants may exhibit distinctive morphological characteristics that were thought to be adaptive under these conditions

(Briske 1996). These adaptive features typically couple with changes in plant architecture (Smith 1998) and in resource allocation patterns (Jaramillo and Detling 1988; Erneberg 1999). Grazing defoliation usually reduces growth rate, reproduction and biomass of the aboveground part (Belsky 1986; Crawley 1997; Erneberg 1999) and increases biomass of the belowground part of plants (Erneberg 1999; Paige 1999). Only a few studies showed no or only a small decrease in plant size and reproduction (Karban and Courtney 1987; Reichman and Smith 1991; Bråthen and Odasz-Albrigtsen 2000). A well-known fact is that the greater the risk (i.e. where there is a high probability of a large or frequent loss), the more a plant should store resources to support future growth and reproduction (Dafni et al. 1981; Chapin et al. 1990). Under these conditions, allocation decisions would give rise to the physiological trade-offs between storage,

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*Author for correspondence.

Tel: +86 29 8531 0266

Fax: +86 29 8531 0546

E-mail: <zhuzhihong@snnu.edu.cn>.

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growth and reproduction of individual plants (Stearns 1992). However, the way in which allocation patterns change with grazing pressures is still not clear. Synchronously, selection by herbivores may create sufficient environmental variability (Ward and Saltz 1994) to affect the allocation pattern that is adapted as a result of the damage experienced by the plant (Ruiz et al. 2002). Therefore, selection exerted by herbivores interacts with resource availability results in fitness trade-offs associated with different resource allocation patterns in different environments (Herms and Mattson 1992). So, it is likely that individuals from populations exposed to different long-term grazing pressures may only vary relative allocation to component parts according to herbivore pressure and not vary absolute investment in plant size because there are adaptive allocation patterns. It is therefore reasonable to hypothesize a possibility that grazing can alter relative allocation to different plant parts without changing total biomass for some plant species if there are life history trade-offs between different plant functions.

Grazing by domestic herbivores has both extensive and profound effects on plant communities. Grassland systems can be characterized by a large diversity of plants which is mainly determined by the availability of nutrients and the degree of defoliation (Lavelle et al. 1997). A quantitative analysis of 195 studies from all over the world confirmed that overall grazing favored annuals over perennials, short-statured over tall-statured plants, prostrate over erect plants, and stoloniferous or rosette over tussock architecture (Lavelle et al. 2007). This indicated that there is difference in plant resistant capability to herbivory, and grazing can shift the balance of relative species' abundances and species composition. Some species will decrease consistently in response to increased grazing intensity, while others increase consistently, and some do not respond or only appear above a certain grazing intensity (Noy-Meir et al. 1989). The indices for measuring species diversity of a community, such as the Shannon-Wiener (H') diversity index or the Simpson diversity index etc., combine both species richness and evenness in a single index. Theoretically, we can easily obtain a given diversity value by different combinations of species richness and evenness. Some studies have also indicated that species composition changed markedly under different grazing intensity, but species diversity value changed little (Noy-Meir et al. 1989; Milchunas and Lauenroth 1993; Zhu and Wang 1996; Jauffret and Lavelle 2003; Zhou et al. 2006b). However, research of integrative species diversity with relative species' abundance/composition is still limited. Therefore, we can hypothesize that, at the community scale, increasing grazing pressure will exacerbate the negative effects of grazing to some species and lead to their decrease in relative abundances. Consequently, those species that are more resistant to herbivory will be more likely to remain and increase relative abundances, whereas those that are less resistant will be likely to decrease relative abundances and even become locally extinct from the community when grazing pressures are

over a certain threshold. Hence, the overall effect of grazing on species composition of community (in terms of species diversity) may be neutral within a range of grazing pressures. If so, perhaps only relative species' abundances or species composition can be altered, and species diversity cannot vary when the same communities are exposed to different long-term grazing pressures.

To test these hypotheses, we carried out a livestock grazing experiment to evaluate species and community response to long-term grazing (12 years) of an alpine shrub meadow on the north-eastern Qinghai-Tibetan Plateau, a region highly vulnerable to ongoing climate and land use changes (Klein et al. 2004). Overgrazing resulting from human activity has led to degradation of 30% of the pasturelands in the region (Zhao and Zhou 1999; Wang et al. 2006) and its effect has caused increasing concern during recent decades because of the rapid increase in livestock numbers (Zhou et al. 2006a). Studies on the effects of long-term grazing at both the individual plant level and the community level in vulnerable regions of the world can add greatly to our ability to model and predict vegetative responses to human land resource use patterns (Klein et al. 2004).

In the study area, the most important and dominant grazers are Tibetan sheep and yak, which are domestic animals. For the last 50 years most of the area has been grazed by Tibetan sheep and yak at moderate to high intensities (Wang Dexu, pers. comm., 1991). Alpine shrubland communities are widespread on north-facing hill slopes, usually at elevations 3 150–3 800 m in the study area. The soil is alpine shrub meadow soil (Yang 1982). The dominant species, *Potentilla fruticosa* is about 30–80 cm; the community cover is about 60%–80%. The main accompanying herbaceous plants are *Leontopodium nanum*, *Potentilla discolor*, *Stipa aliena*, *Potentilla viviparum*, *Festuca rubra*, *Kobresia capillifolia* and *Saussurea nigrescens*, and the net aboveground primary production (NAPP) of the community was 176.1 g dry weight/m² per year (Yang 1982). The target plant *Potentilla viviparum* L. var. *angustum* is a perennial preferred forage herb and is a common sensitivity species that responds to grazing stimulation in the study area. Despite the proportion of aboveground biomass of shrubs, grasses and litter of the community decreasing and forbs (as indicator plants of grassland degradation, are mainly dicotyledonous small herb and mostly unavailable for sheep and yak) increasing as the grazing density increased (Zhao and Zhou 1999), and long-term heavy grazing simplified the structures of alpine shrub community (Zhou et al. 2004), a recent study has shown that alpine meadow ecosystem in the area is still stable (Zhou et al. 2006a). Changes in annual net primary production of the ecosystem was less than that of the annual precipitation and the annual mean air temperature over 40 years. (Zhou et al. 2006a). Many studies have neglected accompanying herbaceous plants' effects in communities in many years past. In fact, accompanying species may be very important to maintain species diversity of communities. We consider that the changes of relative species'

abundances or species composition under different grazing intensities are very important to keep the stability of the alpine meadow ecosystem. Some relevant questions we asked are as follows: (i) whether total plant size of *Polygonum viviparum* L. var. *angustum* would remain constant across a grazing pressure gradient; (ii) how patterns of resource allocation of *Polygonum viviparum* L. var. *angustum* would change in relation to grazing pressure; (iii) whether there is any evidence of life history trade-offs between plant traits; and (iv) whether grazing would shift relative species' abundance or species composition and not vary species diversity?

Results

Effect of treatments on morphological traits of *P. viviparum* L. var. *angustum*

Although there were significant effects of treatments on measured traits after long-term grazing defoliation (Table 1, Figure 1), as expected, total plant dry mass did not differ among treatments in either year. Stem height and aboveground mass of plants decreased significantly with increasing grazing pressure (Figure 1A,B). Heavy grazing pressure resulted in greater belowground mass (Figure 1C). Stem mass significantly decreased with increasing grazing pressure (Figure 1D). Mean bulbil mass and bulbil numbers per plant significantly decreased with grazing pressures (Figure 1E,F). Leaf numbers per plant did not differ among grazing treatments. No difference was found among treatments in mean leaf mass and stem numbers per plant in 2000. But in 2001, the result of multiple comparisons by Tukey's post-hoc test showed no significant difference in mean leaf mass ($P=0.384$) and in stem numbers per plant ($P=0.404$) among treatments, although the difference among treatments was significant by using MANOVA.

Biomass allocation of *P. viviparum* L. var. *angustum*

Grazing greatly affected biomass allocation to reproductive, storage and growth function of *P. viviparum* L. var. *angustum* (Table 2). Both reproductive and growth allocation decreased while storage allocation increased with increasing grazing pressure (Figure 2). Storage and reproductive allocation were negatively correlated within and among treatments, as were growth and storage allocations (Table 3). The same situation was found between bulbil numbers and mean bulbil mass. Especially in 2001, bulbil numbers were negatively related with bulbil mass within and among treatments. Signs of correlation were uniform between bulbil numbers and mean bulbil mass within and among treatments in 2000, although there was only a significant correlation between them in light grazing treatment (Table 3). Growth and reproductive allocation were positively correlated within and among treatments in both years (Table 3).

Effect of treatments on species composition and species response to grazing

Table 4 shows the species list included in the study and their response types to grazing using curve estimation methods for the summed dominance ratio (SDR) of species (Y) to grazing intensity (X). Approximately 69 species were recorded; only 13 were statistically significant ($P \leq 0.05$). In another 10 species, marginally significant differences ($0.05 < P \leq 0.10$) were recorded. Another 46 species (66.67%) that did not differ among grazing treatments ($P > 0.10$) were neutral. Species distribution among species groups defined initially by growth form and plant height was 3, 9, 15 and 42 for shrubs, tall herbs, medium herbs and small herbs, respectively (Tables 4, 5). The recorded number of species was 59, 58 and 57 at light grazing, moderate grazing and heavy grazing treatments, respectively. The percentage of co-occurring species was 77.96%, 79.31% and 80.70% at light grazing, moderate grazing and heavy grazing treatments, respectively. This represents a difference in species composition of about 18%–20% among grazing treatments. These differential species are often small herbs and their SDR usually less than 1.00% (Table 4). Moreover, the dominant and subdominant species at light grazing treatments were *P. fruticosum* (11.85% SDR), *L. nanum* (9.51%), *P. discolor* (7.07%), *F. rubra* (6.81%), *S. aliena* (6.24%) and *Anaphalis lactea* (6.01%); those for moderate grazing were *Lancea tibetica* (11.26%), *L. nanum* (9.97%), *P. discolor* (7.71%), *P. fruticosum* (6.50%), and *Thalictrum alpinum* (6.22%), and for heavy grazing were *P. discolor* (7.61%), *T. alpinum* (7.27%), *Trollius farreri* (6.04%), *S. aliena* (5.92%), *L. nanum* (5.75%) and *P. fruticosum* (5.12%) (Table 4).

All species were accounted for by the combination of grazing increasers (5.80%), grazing decreaseers (11.59%), neutral species (66.67%) and species with mixed responses (15.94%) (Table 5). Fifty-eight (84.06%) species consistently responded to increasing grazing (i.e. increasers, decreaseers and neutral). In grazing increasers, small herbs and medium herbs accounted for 75.00% and 25.00%, respectively. In grazing decreaseers, shrubs and small herbs accounted for 12.50% and 37.50%, respectively, and tall herbs accounted for the same 25.00% as medium herbs. Neutral, shrubs, tall herbs and medium herbs together accounted for 32.61%, whereas small herbs contributed 67.39%. In species with mixed responses, and which consist of herbs, 45.45%, 36.37% and 18.17% of them were small herbs, medium herbs, and tall herbs, respectively (Table 5).

Species groups' response to grazing

Summed dominance ratio of both shrub groups and herb groups was greatly affected by grazing (Table 6). Herbs' SDR increased while shrubs' SDR decreased with increased grazing pressure. There was a completely negative relationship between them (Table 7). However, in the herb group, tall herbs' SDR didn't

Table 1. MANOVA for effects of grazing treatments on morphological and biomass traits of *Polygonum viviparum* L. var. *angustum* in 2000 and 2001

Traits	Source of variation	2000				2001			
		<i>df</i>	<i>MS</i> ^a	<i>F</i>	<i>P</i>	<i>df</i>	<i>MS</i> ^a	<i>F</i>	<i>P</i>
Stem height	Treatment	2	0.601	29.712	0.000	2	0.325	14.248	0.000
	Block	2	0.063	0.310	0.068	2	0.120	5.263	0.016
	Block × treatment	4	0.061	2.995	0.047	4	0.067	2.954	0.049
	Error	18	0.020			18	0.023		
	Total	26				26			
Total dry mass	Treatment	2	0.187	2.755	0.090	2	0.018	0.302	0.743
	Block	2	0.076	1.122	0.347	2	0.291	4.835	0.021
	Block × treatment	4	0.089	1.321	0.300	4	0.151	2.514	0.078
	Error	18	0.068			18	0.060		
	Total	26				26			
Aboveground mass	Treatment	2	0.809	18.727	0.000	2	0.352	5.085	0.018
	Block	2	0.073	1.699	0.211	2	0.352	5.088	0.018
	Block × treatment	4	0.092	2.119	0.120	4	0.136	1.967	0.143
	Error	18	0.043			18	0.069		
	Total	26				26			
Below ground mass	Treatment	2	0.468	3.602	0.050	2	0.284	3.650	0.047
	Block	2	0.099	0.764	0.480	2	0.302	3.852	0.040
	Block × treatment	4	0.109	0.839	0.519	4	0.192	2.454	0.083
	Error	18	0.130			18	0.078		
	Total	26				26			
Mean stem mass	Treatment	2	0.744	6.697	0.007	2	0.430	6.287	0.008
	Block	2	0.296	2.665	0.097	2	0.911	13.301	0.000
	Block × treatment	4	0.079	0.712	0.594	4	0.139	2.026	0.134
	Error	18	0.111			18	0.068		
	Total	26				26			
Mean bulbil mass	Treatment	2	0.049	9.047	0.002	2	0.015	3.575	0.048
	Block	2	0.005	0.947	0.406	2	0.034	7.917	0.003
	Block × treatment	4	0.005	0.868	0.502	4	0.010	2.271	0.102
	Error	18	0.005			18	0.004		
	Total	26				26			
Mean leaf mass	Treatment	2	0.161	2.666	0.097	2	0.165	4.861	0.021
	Block	2	0.069	1.134	0.344	2	0.085	2.514	0.109
	Block × treatment	4	0.077	1.274	0.317	4	0.131	3.856	0.020
	Error	18	0.060			18	0.034		
	Total	26				26			
Stem numbers	Treatment	2	0.030	2.788	0.088	2	0.083	3.631	0.047
	Block	2	0.009	0.885	0.430	2	0.001	0.011	0.989
	Block × treatment	4	0.008	0.719	0.590	4	0.017	0.745	0.574
	Error	18	0.011			18	0.023		
	Total	26				26			
Bulbil numbers	Treatment	2	6.339	5.298	0.016	2	2.882	4.195	0.037
	Block	2	0.518	0.433	0.655	2	0.766	1.115	0.349
	Block × treatment	4	0.841	0.703	0.600	4	0.499	0.726	0.586
	Error	18	1.196			18	0.687		
	Total	26				26			
Leaf numbers	Treatment	2	0.038	0.680	0.519	2	0.030	1.006	0.385
	Block	2	0.060	1.087	0.358	2	0.162	5.376	0.015
	Block × treatment	4	0.088	1.587	0.221	4	0.021	0.679	0.615
	Error	18	0.055			18	0.030		
	Total	26				26			

^aMean square calculated from Type III sums of squares.

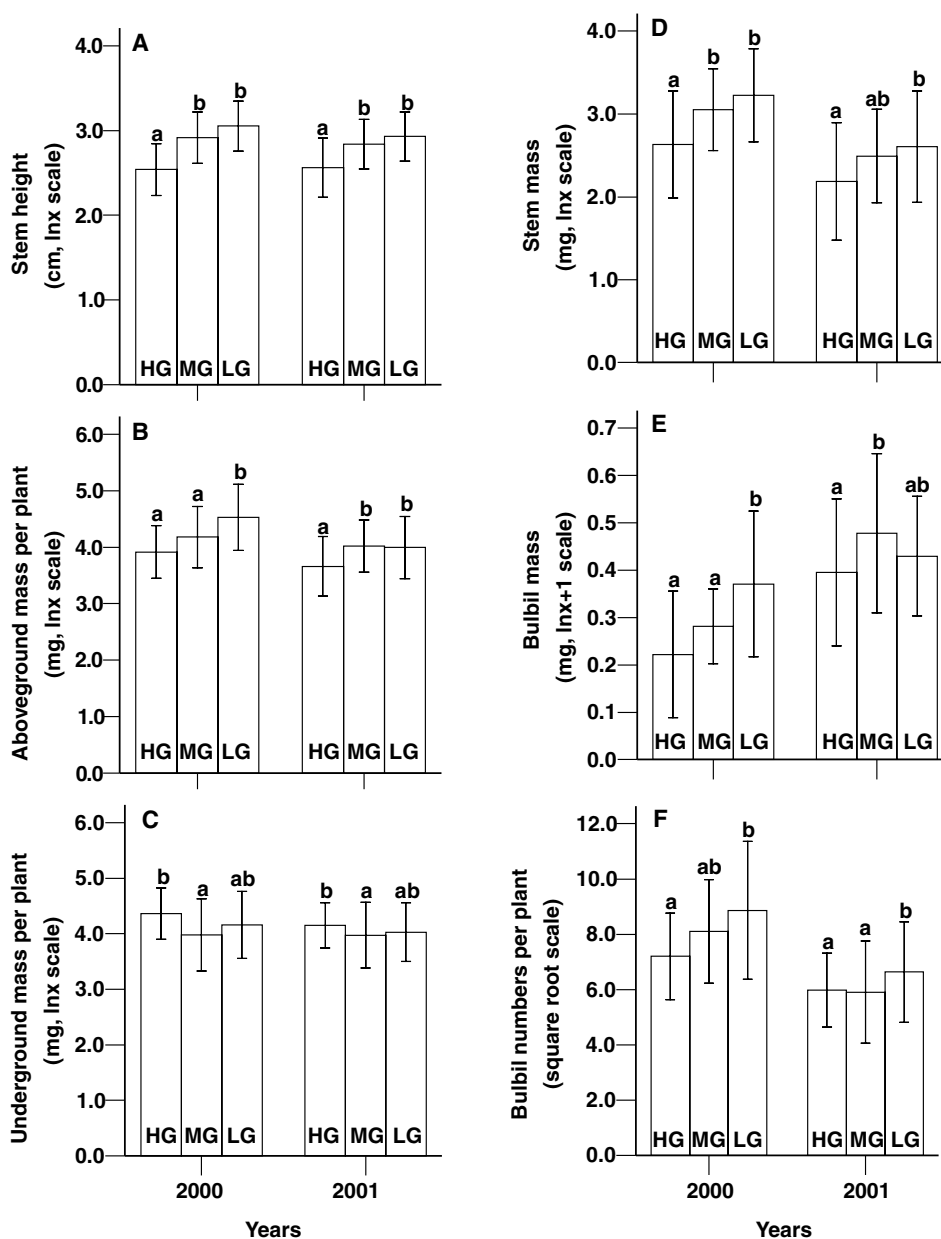


Figure 1. Effects of grazing treatments on morphological and biomass traits (mean \pm 1.0 SD) of *Polygonum viviparum* L. var. *angustum* in 2000 and 2001.

Multiple comparisons were carried out among grazing treatments with Tukey's post-hoc tests. Same letters above bars indicate non-significant differences ($P > 0.05$) among treatments within each year, and different letters indicate significant differences ($P \leq 0.05$). HG, heavy grazing; LG, light grazing; MG, moderate grazing.

differ among treatments. Medium herbs' SDR and small herbs' SDR showed mixed responses to grazing (Table 6). Curve regressions for SDR (Y) showed concave curve responses to grazing intensity (X) in medium herbs, and convex curve responses in small herbs, respectively (Figure 3). There was a strong positive relationship across grazing treatments between

the SDR of small herbs and that of all herbs, and a negative relationship with that of shrubs, tall herbs and medium herbs, respectively (Table 7). This suggested that changes in relative species' abundance of the community was mainly determined by comparative changes of species' abundance between small herbs and other species groups with grazing pressures.

Table 2. ANCOVA for effects of grazing treatments on biomass allocation to different plant organs of *Polygonum viviparum* L. var. *angustum* with total plant size as a covariate

Allocation traits	Source of variation	2000				2001			
		df	MS ^a	F	P	df	MS ^a	F	P
Reproductive allocation	Plant size	1	0.006	4.454	0.050	1	0.001	0.952	0.343
	Treatment	2	0.030	24.036	0.000	2	0.005	3.594	0.048
	Block	2	0.001	0.468	0.634	2	0.001	0.618	0.551
	Block × treatment	4	0.003	2.742	0.063	4	0.001	0.429	0.786
	Error	17	0.001			17	0.001		
	Total	26				26			
Storage allocation	Plant size	1	0.005	1.497	0.238	1	0.017	8.004	0.012
	Treatment	2	0.059	16.928	0.000	2	0.018	8.210	0.003
	Block	2	0.006	1.805	0.195	2	0.007	3.400	0.057
	Block × treatment	4	0.003	0.771	0.559	4	0.005	2.410	0.090
	Error	17	0.003			17	0.002		
	Total	26				26			
Growth allocation	Plant size	1	0.009	5.049	0.038	1	0.000	0.185	0.673
	Treatment	2	0.029	16.904	0.000	2	0.008	3.859	0.042
	Block	2	0.000	0.039	0.961	2	0.000	0.125	0.883
	Block × treatment	4	0.002	1.242	0.330	4	0.001	0.281	0.886
	Error	17	0.002			17	0.002		
	Total	26				26			

^a Mean square calculated from Type III sums of squares.

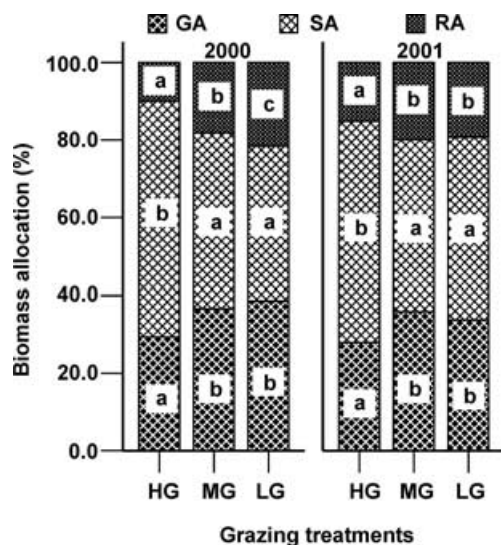


Figure 2. Biomass allocation response of *Polygonum viviparum* L. var. *angustum* to grazing intensity in 2000 and 2001.

Adjustments for multiple comparisons were carried out using Bonferroni correction. Same letters inside bars indicate non-significant difference ($P > 0.05$) among treatments within each year, and different letters indicate significant differences ($P \leq 0.05$). (▨), growth allocation; (▩), storage allocation; (■), reproductive allocation. HG, heavy grazing; LG, light grazing; MG, moderate grazing.

Effect of treatments on species diversity

No differences were found in the species diversity index H' among treatments calculated by whole species, shrubs, whole herbs, tall herbs, and by small herbs, respectively, except by medium herbs, which was higher at light grazing treatment than in other treatments (Table 6). The same situation was found in the evenness index E . However, there was significant difference in species richness (SR) among treatments, and heavy grazing resulted in significantly greater SR than light grazing: about 4.5 species. This represents a 13.2% decline in SR from heavy grazing to light grazing.

Discussion

Evaluation regarding effects of grazing on *P. viviparum* L. var. *angustum*

Total plant biomass of *P. viviparum* L. var. *angustum* did not vary with grazing pressures even though individual plant morphological characters were modified by long-term herbivory (Table 1). The results support our hypothesis that individual plants only vary their relative allocation to their component parts across different grazing pressures, not their absolute investment in size. Whole differences in plant traits of the species

Table 3. Pearson correlations between allocation traits of *Polygonum viviparum* L. var. *angustum* within and among treatments in 2000 and 2001

Correlation variables		Treatments	2000		2001	
			<i>r</i>	<i>N</i> ^b	<i>r</i>	<i>N</i>
Storage allocation	Reproductive allocation	HG	−0.577**	21	−0.451**	49
		MG	−0.763**	37	−0.621**	29
		LG	−0.455*	30	−0.760**	34
		Among ^a	−0.699**	88	−0.603**	112
Growth allocation	Reproductive allocation	HG	0.677**	21	0.640**	49
		MG	0.666**	37	0.941**	29
		LG	0.845**	30	0.759**	34
		Among	0.803**	88	0.839**	112
Growth allocation	Storage allocation	HG	−0.813**	21	−0.773**	49
		MG	−0.831**	37	−0.683**	29
		LG	−0.719**	30	−0.936**	34
		Among	−0.832**	88	−0.780**	112
Bulbil numbers	Bulbil mass	HG	−0.189 <i>ns</i>	21	−0.466**	49
		MG	−0.021 <i>ns</i>	37	−0.505**	29
		LG	−0.380*	30	−0.296*	34
		Among	−0.082 <i>ns</i>	88	−0.405**	112

^aLinear regression among treatments. ^b*n* is the sample sizes used as analysis. HG, heavy grazing; LG, light grazing; MG, moderate grazing; **P* < 0.05; ***P* < 0.01. *ns* = not significant (*P* > 0.05).

among treatments may represent an adaptive grazing avoidance strategy after long-term grazing selection. For example, plants reduced the resources investment in stem height, bulbil number, bulbil mass and in allocation biomass to aboveground parts, and increased the resources in rhizome mass and in allocation biomass to belowground parts with increasing grazing pressure (Figures 1, 2). The strategy is important to reduce grazing severity and to promote long-term persistence of the species in the community. Meanwhile, the differences in soil nutrients or other environmental factors among treatments by long-term herbivory may also induce relative responses. In the area, stocking rates are negatively correlated with organic matter, organic carbon, total nitrogen and total phosphorus of the soil (Dong et al. 2004). Soil nitrogen availability decreased with increasing grazing pressure and didn't meet the growth demand of grasses and sedges, but still met the demand of forbs (Chao et al. 2004). This suggested that the forbs may have lower soil nitrogen demand and higher tolerance ability to scarcity of soil nitrogen than grasses and sedges. In our study, *P. viviparum* L. var. *angustum*, a perennial preferred forage forb, became shorter and allocated less biomass to aboveground parts due to the higher risk of herbivory, but lower soil nitrogen availability in heavy grazing treatment did not limit directly absolute investment in total plant size; the plant just allocated more available resources to the belowground part. It

is also possible that the shifts observed truly reflect an adaptive response to long term defoliation, because in years prior to the study where all plants were available to grazers and sample plants had not been defoliated by herbivory within the current growing season, plants were covered with a cube-shaped wire frame in early spring until the sampling date. Thus the allocation responses and morphological changes observed represents long-term grazing effects, rather than short-term responses of individuals after damage.

The expectation that life history trade-offs would occur among the competing functions was upheld by the negative relationships (Table 3). Even as Lehtila (1999) suggested that the build-up of storage incurs costs and decreases growth rate. The principle of allocation assumes that limiting resources are allocated to different functions in a more or less optimal way and patterns of resource allocation reflect the adaptive importance of life-history traits (Lovett Doust 1989). Our result suggests that long-term grazing would affect resource allocation between above- and below-ground parts, and the evolution of traits that determine growth, reproduction and storage function of the species. So the argument that the plant-herbivore association can be mutualistic (McNaughton 1986; Paige and Whitham 1987; Paige 1992; Vail 1992; Paige 1999) may be untenable, because any benefit from herbivore damage was attained at an evolutionary cost (Simons and Johnston 1999).

Table 4. Species list included in the study and their response to livestock grazing with curve estimation method for species' summed dominance ratio (SDR) (Y) to grazing intensity (X)

Grazing responses	Species	Species' SDR			Models	Species groups	
		LG	MG	HG			
GR	<i>Trollius farreri</i>	0.20	0.00	6.24	$Y = -5.487 + 1.861X, R^2 = 0.384,$ $F_{1,25} = 15.577, P = 0.001$	Medium herb	
	<i>Taraxacum monogolicum</i>	0.27	0.77	1.59	$Y = -0.954 + 0.451X, R^2 = 0.264,$ $F_{1,25} = 8.948, P = 0.006$	Small herb	
	<i>Saussurea superba</i>	0.70	2.81	3.28	$Y = 5.708 - 12.721/X, R^2 = 0.163,$ $F_{1,25} = 4.854, P = 0.037$	Small herb	
	<i>Oxytropis ochrocephala</i>	1.60	2.26	2.76	$Y = 0.542 + 0.408X, R^2 = 0.105,$ $F_{1,25} = 2.935, P = 0.099^*$	Small herb	
GD	<i>Potentilla fruticosa</i>	11.85	6.50	5.82	$Y = -1.096 + 32.985/X, R^2 = 0.220,$ $F_{1,25} = 7.063, P = 0.014$	Shrub	
	<i>Helictotrichon tibeticum</i>	0.90	0.66	0.00	$Y = 1.795 - 0.304X, R^2 = 0.127,$ $F_{1,25} = 3.650, P = 0.068^*$	Tall herb	
	<i>Morina chinensis</i>	0.53	0.14	0.02	$Y = -0.426 + 2.453/X, R^2 = 0.107,$ $F_{1,25} = 3.004, P = 0.095^*$	Tall herb	
	<i>Anaphalis hancockii</i>	0.21	0.04	0.00	$Y = -0.195 + 1.027/X, R^2 = 0.143,$ $F_{1,25} = 4.172, P = 0.052^*$	Medium herb	
	<i>Thermopsis lanceolata</i>	3.39	0.05	0.03	$Y = -3.585 + 17.541/X, R^2 = 0.445,$ $F_{1,25} = 20.026, P = 0.000$	Medium herb	
	<i>P. viviparum</i> L. var. <i>angustum</i>	0.67	0.17	0.04	$Y = -0.406 + 2.715/X, R^2 = 0.183,$ $F_{1,25} = 5.595, P = 0.026$	Small herb	
	<i>Euphrasia pectinata</i>	3.04	1.71	1.38	$Y = -0.159 + 8.154/X, R^2 = 0.140,$ $F_{1,25} = 4.075, P = 0.054^*$	Small herb	
	<i>Arenaria kansuensis</i>	0.31	0.06	0.01	$Y = -0.264 + 1.448/X, R^2 = 0.149,$ $F_{1,25} = 4.362, P = 0.047$	Small herb	
	CONVEX	<i>Ptilagrostis dichotoma</i>	0.17	0.65	0.15	$Y = -3.468 + 2.116X - 0.269X^2,$ $R^2 = 0.174, F_{2,24} = 2.536, P = 0.100^*$	Tall herb
		<i>Anemone obtusiloba</i>	1.99	3.33	0.17	$Y = -14.744 + 9.999X - 1.348X^2,$ $R^2 = 0.447, F_{2,24} = 9.682, P = 0.004$	Medium herb
<i>Koeleria cristata</i>		0.52	0.96	0.11	$Y = -4.252 + 2.841X - 0.379X^2,$ $R^2 = 0.198, F_{2,24} = 2.970, P = 0.070^*$	Medium herb	
<i>Lancea tibetica</i>		3.04	11.26	5.06	$Y = -50.451 + 30.643X - 3.787X^2,$ $R^2 = 0.492, F_{2,24} = 11.627, P = 0.000$	Small herb	
<i>Gueldenstaedtia diversifolia</i>		0.74	3.32	0.75	$Y = -18.345 + 11.057X - 1.399X^2,$ $R^2 = 0.269, F_{2,24} = 4.412, P = 0.023$	Small herb	
<i>Rubia cordifolia</i>		0.14	0.63	0.00	$Y = -4.019 + 2.431X - 0.314X^2,$ $R^2 = 0.178, F_{2,24} = 2.597, P = 0.095^*$	Small herb	
CONCAVE	<i>Kobresia capillifolia</i>	1.74	0.81	3.45	$Y = 15.010 - 7.972X + 1.086X^2,$ $R^2 = 0.208, F_{2,24} = 2.870, P = 0.085^*$	Tall herb	
	<i>Festuca rubra</i>	6.81	1.25	2.51	$Y = 17.933 - 7.951X + 0.947X^2,$ $R^2 = 0.223, F_{2,24} = 3.454, P = 0.048$	Medium herb	
	<i>Anaphalis lacteal</i>	6.01	2.01	3.81	$Y = 27.584 - 12.112X + 1.432X^2,$ $R^2 = 0.216, F_{2,24} = 3.310, P = 0.054^*$	Medium herb	
	<i>Gentiana squarrosa</i>	0.06	0.00	1.09	$Y = 4.390 - 2.679X + 0.386X^2, R^2 = 0.316,$ $F_{2,24} = 5.549, P = 0.010$	Small herb	
	<i>Iris goniocarpa</i>	0.68	0.06	1.13	$Y = 6.947 - 3.702X + 0.489X^2, R^2 = 0.222,$ $F_{2,24} = 3.416, P = 0.049$	Small herb	

Table 4. (continued)

Grazing responses	Species	Species' SDR			Models	Species groups
		LG	MG	HG		
NE	<i>Spiraea alpina</i>	0.04	0.10	0.16		Shrub
	<i>Salix oritrepha</i>	0.00	0.00	0.15		Shrub
	<i>Elymus nutans</i>	0.74	1.11	0.68		Tall herb
	<i>Ptilagrostis concinna</i>	0.04	0.00	0.03		Tall herb
	<i>Deyeuxia flavens</i>	0.00	0.19	0.00		Tall herb
	<i>Gentianopsis paludosa</i>	0.29	0.21	0.06		Tall herb
	<i>Notopterygium forbesii</i>	0.72	0.41	0.60		Tall herb
	<i>Stipa aliena</i>	6.24	3.74	5.92		Medium herb
	<i>Polygonum viviparum</i>	1.96	5.23	3.89		Medium herb
	<i>Festuca ovina</i>	3.20	1.74	2.67		Medium herb
	<i>Ligularia virgaurea</i>	0.39	0.00	2.46		Medium herb
	<i>Aster flaccidus</i>	0.95	1.45	1.18		Medium herb
	<i>Poa orinosa</i>	0.80	0.78	0.36		Medium herb
	<i>Ligularia sagitta</i>	0.00	0.19	0.00		Medium herb
	<i>Stellera chamaejasme</i>	0.00	0.12	0.00		Medium herb
	<i>Thalictrum alpinum</i>	5.05	6.22	7.27		Small herb
	<i>Gentiana lawrencei</i>	2.03	5.22	4.01		Small herb
	<i>Potentilla discolor</i>	7.07	7.71	7.61		Small herb
	<i>Kobresia humilis</i>	2.15	2.59	3.08		Small herb
	<i>Leontopodium nanum</i>	9.51	9.97	5.75		Small herb
	<i>Saussurea nigrescens</i>	4.19	1.99	2.99		Small herb
	<i>Geranium pylzowianum</i>	2.34	1.09	1.29		Small herb
	<i>Carex atrofusca</i>	0.43	1.46	1.25		Small herb
	<i>Parnassia trinervis</i>	0.83	0.51	1.24		Small herb
	<i>Gentiana aristata</i>	1.97	2.48	1.61		Small herb
	<i>Swertia tetraptera</i>	1.29	0.61	0.62		Small herb
	<i>Scirpus distigmaticus</i>	1.47	3.19	1.95		Small herb
	<i>Pedicularis kansuensis</i>	0.58	0.25	0.52		Small herb
	<i>Pyrola calliantha</i>	0.91	0.05	1.18		Small herb
	<i>Galium verum</i>	0.00	0.11	0.01		Small herb
	<i>Gentiana straminea</i>	0.86	0.62	0.57		Small herb
	<i>Leontopodium longifolium</i>	0.05	0.00	0.93		Small herb
	<i>Ranunculus tanguticus</i>	0.01	0.00	0.00		Small herb
	<i>Ranunculus pulchellus</i>	0.15	0.15	0.36		Small herb
	<i>Galium aparine</i>	0.28	0.01	0.20		Small herb
	<i>Potentilla anserina</i>	0.26	0.00	0.38		Small herb
	<i>Potentilla bifurca</i>	0.13	0.35	0.02		Small herb
	<i>Saussurea kokonorensis</i>	0.13	0.04	0.00		Small herb
	<i>Astragalus</i> sp.	0.06	0.15	0.01		Small herb
	<i>Torularia humilis</i>	0.03	0.00	0.00		Small herb
<i>Stellaria media</i>	0.02	0.00	0.03		Small herb	
<i>Saxifraga montana</i>	0.00	0.00	0.03		Small herb	
<i>Pedicularis</i> sp.	0.00	0.09	0.00		Small herb	
<i>Pedicularis alaschanica</i>	0.00	0.13	0.02		Small herb	
<i>Ranunculus hirtellus</i>	0.00	0.08	0.00		Small herb	
<i>Carex moorcroftii</i>	0.00	0.01	0.00		Small herb	

All recorded species in the study were divided into four groups, namely shrub, tall herb (>40 cm at maturity), medium herb (20–40 cm) and small herb (<20 cm), according to growth form and plant height (Noy-Meir et al. 1989; Díaz et al. 2001). Grazing responses were divided into five types: CONCAVE, concave curve response; CONVEX, convex curve response; GD, grazing decrease; GR, grazing increase; NE, neutral. HG, heavy grazing; LG, light grazing; MG, moderate grazing. *Data are referred to as marginally significant for $0.05 < P \leq 0.10$.

Table 5. Cross-tabulation of the sixty-nine species by grazing response type and by species groups

Species groups	Consistent responses			Inconsistent responses		Total
	Increasesers	Decreasers	Neutral	Convex	Concave	
Shrubs	0 (0, 0)	1 (12.5%, 33.3%)	2 (4.3%, 66.7%)	0 (0, 0)	0 (0, 0)	3 (4.3%)
Tall herbs	0 (0, 0)	2 (25.0%, 22.2%)	5 (10.8%, 55.6%)	1 (16.6%, 11.1%)	1 (20.0%, 11.1%)	9 (13.1%)
Medium herbs	1 (25.0%, 6.7%)	2 (25.0%, 13.3%)	8 (17.3%, 53.3%)	2 (33.3%, 13.3%)	2 (40.0%, 13.3%)	15 (21.8%)
Small herbs	3 (75.0%, 7.1%)	3 (37.5%, 7.1%)	31 (67.3%, 73.8%)	3 (50.0%, 7.1%)	2 (40.0%, 4.7%)	42 (60.8%)
Total	4 (5.8%)	8 (11.6%)	46 (66.7%)	6 (8.7%)	5 (7.2%)	69 (100.0%)

Numbers (and percentage of column totals, percentage of row totals) indicate the number of species of a particular grazing response type within a species group. Grazing response type was determined by curve regressions using curve estimation method for each species' summed dominance ratio (SDR) (Y) to grazing intensity (X) across grazing intensity.

Table 6. MANOVA for species richness (SR), species diversity (H'), evenness index (E) and summed dominance ratio (SDR) of species groups and the results of multiple comparisons among grazing treatments with Tukey's post-hoc tests

Index	Characteristics of species groups	Grazing intensity (Tibetan sheep/ha)			$F_{2,18}$	Significance
		LG	MG	HG		
SR		29.67 ± 3.64 ^a	32.89 ± 2.26 ^{ab}	34.22 ± 3.31 ^b	5.796	0.011
H'	Overall species H'	2.81 ± 0.16 ^a	2.97 ± 0.09 ^a	2.98 ± 0.17 ^a	2.930	0.079
	Shrubs H'	0.05 ± 0.17 ^a	0.10 ± 0.20 ^a	0.14 ± 0.28 ^a	0.290	0.752
	Herbs H'	2.94 ± 0.09 ^a	2.78 ± 0.14 ^a	2.94 ± 0.18 ^a	3.351	0.058
	Tall herbs H'	0.96 ± 0.30 ^a	0.88 ± 0.27 ^a	0.71 ± 0.29 ^a	1.949	0.171
	Medium herbs H'	1.88 ± 0.18 ^b	1.47 ± 0.24 ^a	1.66 ± 0.19 ^a	8.915	0.002
	Small herbs H'	2.41 ± 0.11 ^a	2.38 ± 0.18 ^a	2.53 ± 0.21 ^a	1.613	0.227
E	Overall species E	0.60 ± 0.06 ^a	0.58 ± 0.11 ^a	0.58 ± 0.69 ^a	0.161	0.853
	Shrubs E	0.03 ± 0.01 ^a	0.04 ± 0.01 ^a	0.04 ± 0.01 ^a	0.746	0.489
	Herbs E	0.58 ± 0.06 ^a	0.55 ± 0.09 ^a	0.56 ± 0.07 ^a	0.225	0.801
	Tall herbs E	0.08 ± 0.02 ^a	0.08 ± 0.02 ^a	0.06 ± 0.02 ^a	3.350	0.059
	Medium herbs E	0.20 ± 0.03 ^b	0.15 ± 0.03 ^a	0.16 ± 0.03 ^a	6.561	0.008
	Small herbs E	0.34 ± 0.05 ^a	0.37 ± 0.09 ^a	0.38 ± 0.06 ^a	0.642	0.539
SDR	Shrubs SDR	11.90 ± 7.31 ^b	6.60 ± 6.40 ^{ab}	5.44 ± 3.35 ^a	3.841	0.041
	Herbs SDR	88.09 ± 7.31 ^a	93.39 ± 6.40 ^{ab}	94.55 ± 3.35 ^b	3.841	0.041
	Tall herbs SDR	5.16 ± 3.12 ^a	4.23 ± 1.87 ^a	5.02 ± 4.21 ^a	0.309	0.738
	Medium herbs SDR	29.73 ± 9.93 ^b	20.93 ± 8.62 ^a	29.20 ± 6.12 ^b	4.193	0.032
	Small herbs SDR	53.19 ± 7.55 ^a	68.23 ± 9.61 ^b	60.32 ± 10.52 ^{ab}	6.582	0.007

HG, heavy grazing; LG, light grazing; MG, moderate grazing. Non-significant differences between treatments are marked by the same letters and significant differences by different letters. Sixty-nine species were divided into four species groups according to plant growth form (Noy-Meir et al. 1989) (see Tables 4, 5).

Evaluation regarding grazing at species and community level

Grazing response at the community level can be represented by species' and species groups' response to grazing. Our study showed multifarious types of response to grazing either for single species or for species groups (Tables 4, 5). As a result of the SDR of the shrub group decreasing, while that of the herb group increased consistently in response to increased grazing pressure, in general, they can be classified as grazing 'decreasers' and grazing 'increasers', respectively. However, there are three types of responses to grazing within a herb group: the tall herb group is neutral, the small herb group is made up of 'increasers' or convex responses to grazing, and the

medium herb group has a concave response to grazing (Table 6; Figure 3) although only five species of the medium herb group showed the concave response (Table 4). Therefore, the community height reduced due to changes in the relative species' abundance with increasing grazing pressures. The results were consistent in many aspects with the classical predictions of responses to grazing at the species and community level, such as grazing 'increasers' mainly consisted of small herbs and did not have shrubs or tall herbs. But we also detected some differences in response to grazing between single species and species group. For example, not every shrub or 'Tall' plant is a grazing 'decreaser' although the shrub group can be classified as decreasers. Similarly, not every small herb is a grazing 'increaser' (Tables 5, 6). We consider that this phenomenon was

Table 7. Pearson correlation analysis to summed dominance ratio (SDR) of different species groups in alpine shrub community

Species groups	Herbs' SDR	Shrubs' SDR	Tall herbs' SDR	Medium herbs' SDR
Shrubs' SDR	$r = -1.000^{**}$ $P = 0.000$			
Tall herbs' SDR	$r = -0.214$ $P = 0.284$	$r = 0.214$ $P = 0.284$		
Medium herbs' SDR	$r = 0.182$ $P = 0.364$	$r = -0.182$ $P = 0.364$	$r = -0.009$ $P = 0.964$	
Small herbs' SDR	$r = 0.495^{**}$ $P = 0.009$	$r = -0.495^{**}$ $P = 0.009$	$r = -0.403^*$ $P = 0.037$	$r = -0.719^{**}$ $P = 0.000$

*Correlation is significant at the 0.05 level (two-tailed). $n = 27$. **Correlation is significant at the 0.01 level.

caused mainly by an accumulative total of SDR of different plant species within a species group. Moreover, we also noticed that there were large numbers of neutral species in the community and 28 species (61%) of them were less than 1.00% in SDR (Table 4). Therefore, as a result of there being multiformal types of responses to grazing and many neutral species in the community, long term grazing merely shifted the balance of relative species' abundances to about 40% of all species without altering species diversity among grazing treatments within the current range of grazing intensity (Table 6). A recent study reported that the species richness and species diversity were not significantly different, though the species composition differed markedly among grazing intensities after 17 years of grazing in an alpine shrubland meadow, with a decrease in palatable grass species and an increase in unpalatable forbs at higher grazing intensities (Zhou et al. 2006b). In addition, our results showed synchronously a 13.2% increase in SR with increasing grazing intensity, and differences in both species composition about 18%–20% (Table 4) and medium herbs' H' among grazing treatments (Table 6). This suggested that livestock grazing can not only alter species composition but also actually affect species diversity of alpine shrubland meadows. Therefore, the whole species diversity index H' cannot fully reveal the changes in species composition of a plant community.

It is common knowledge that an ecosystem or bio-community can tolerate disturbance to some extent, but if the disturbance approaches some thresholds, they would become unstable. It was also reported that overgrazing and other anthropogenic factors resulted in serious degradation of the alpine meadow ecosystem on the Qinghai-Tibetan Plateau in the past 30 years, with an annual rate of degradation of 6.64%–34.45% (Wang and Cheng 2001; Zhou et al. 2006a). In our study, the heavy grazing intensity may already approach the threshold value that can induce degradation of the community because it resulted in a 54.41% decline in the SDR of dominant shrub species *Potentilla fruticosa* and a 13.40% rise in that of small herbs (was mostly forbs) (Table 6). The phenomena may represent an omen of the grassland degradation in the study area. Therefore, we can reasonably consider that if more heavy and large-scale livestock grazing was carried out in the region, an increased and an

obvious variance in species diversity and species composition will occur, and finally lead to degradation of the grassland as an inevitable consequence of overgrazing.

In our study, changes in community environment (including biotic and abiotic) resulting from removing by grazers to the dominant species *P. fruticosa* should also be one of the important factors leading to changes in relative species' abundance and species composition, because those grazing 'increasers' may also benefit from the reduced competition and increased light availability due to grazing defoliation, rather than from growth stimulation by grazing (Díaz et al. 2001).

In conclusion, our results showed that grazing treatments considerably modified the growth form and the patterns of biomass allocation of individual plants, but total biomass remained constant in *Polygonum viviparum* L. var. *angustum*. Long-term grazing may affect evolution of life-history traits of the species. Simultaneously, owing to there being multiformal types of responses of different species to grazing and many neutral species in the community, long-term grazing merely shifted the balance of relative species' abundances without altering whole species diversity among grazing treatments within the current range of grazing intensity. Undeniably, livestock grazing can also potentially affect species diversity of some species groups of alpine shrubland meadow. Understanding herbivore-plant interaction and community change have important implications for conservation and grazing management of rangelands of the Qinghai-Tibet Plateau.

Materials and Methods

Site and species description

We conducted our research at the Haibei Research Station (37°29'N, 101°12'E, 3300 m elevation), which is situated in the northeast of the Qinghai-Tibet Plateau, in a broad NW-SE oriented valley and surrounded by the Qilian Mountains. Mean annual precipitation is 562 mm, over 80% of which falls as rain during the summer growing season from May to September. Mean annual air temperature at the site is -1.6°C ; mean air temperature during the warmest month (July) is 18°C at the

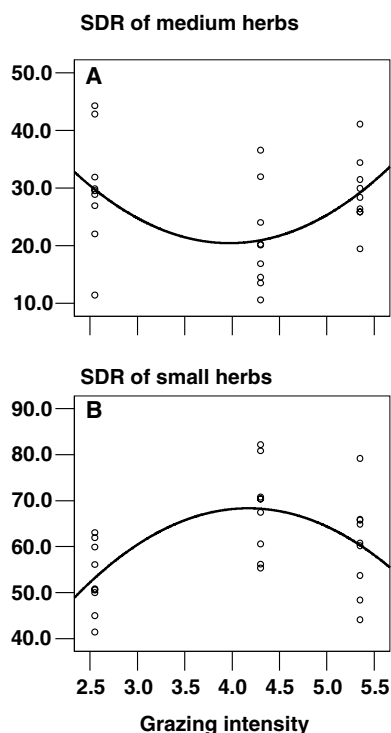


Figure 3. Regression for summed dominance ratio (SDR) (Y) of species groups to grazing intensity (X) with curve estimation method by quadratic model.

(A) Medium herbs. The fitting equation was $Y = 93.108 - 36.605X + 4.609x^2$ ($R = 0.454$, $F_{(2,24)} = 3.121$, $P = 0.062$).

(B) Small herbs. The fitting equation was $Y = -31.853 + 48.035X - 5.758x^2$ ($R = 0.573$, $F_{(2,24)} = 5.875$, $P = 0.008$). (○), observed; (—), quadratic. Sample sizes used as regression analysis is $n = 27$.

valley bottom. Our fenced experimental grazing pasture situated shrubland habitat, a cooler summer-grazed pasture in the region and situates on the higher slopes encircling the valleys, which is dominated by *Potentilla fruticosa* (Yang 1982; Zhang 1990; Zhu and Wang 1996; Zhao and Zhou 1999). Forbs, grasses and sedges occur in the site. *Polygonum viviparum* L. var. *angustum* is usually 3–20 cm high, with <200 mg dry weight. The individual plant has one to four erect un-ramifying stems that directly arise from the short rhizome. The spike is often 1.0–2.5 cm long, with many bulbils and few flowers. Bulbils, a vegetative propagation organ, usually mature during July–August at the study site (Zhu Zhi-Hong, pers. obs., from 1998 to 1999).

Grazing experiment

A fenced experimental grazing pasture was established in April 1988 (5.08 hm^2 area). Experimental grazing pasture had been fenced with seven strands of barbed wire fixed by angle iron posts since 1988. The fence is about 1.20 m in height. A randomized complete block design with three replicates and

three levels of grazing treatments with Tibetan sheep was used. Grazing intensity (in terms of head of Tibetan sheep per hm^2) of the three levels were about 2.55 (light grazing [LG] block area = 0.31 hm^2), 4.30 (moderate grazing [MG] block area = 0.47 hm^2), and 5.35 (heavy grazing [HG] block area = 0.91 hm^2) from 1988 to 1997, respectively. From 1998 to 2001, grazing intensity (in terms of head of Tibetan sheep per hm^2) was about 2.00, 4.00, and 8.00, respectively. The percentages of removed NAPP of pasture for the three treatment levels were about 25%–30% LG, 40%–45% MG, and 60%–70% HG until the end of the grazing period from 1988 to 2001. The grazing period in the present study is 5 months (from 1 June to 31 October) every year and consistent with the free grazing period of farming animals in local summer–autumn pastures.

Sampling

Twenty seven quadrats (1 × 1 m) (three levels × three blocks × three quadrats per block) were randomly located in the experimental pasture in early spring of each year during the study period (from 2000 to 2001). All plant samples of *P. viviparum* L. var. *angustum* were collected from these quadrats during 19–20 July 2000 and 1–2 August 2001. Because the phenological phase of plants in 2001 was later than that in 2000 by about 10–15 d (Zhu Zhi-Hong, pers. obs., from 2000 to 2001), the sampling dates in 2001 were delayed for about 13–14 d in order to ensure a similar growth stage between seasons. In order to reveal the effects of long-term grazing defoliation on the plant, each of the quadrats was covered with a cube-shaped wire frame (1.5 × 1.5 × 0.7 m) in early spring until the sampling date in the study period. Individual plants that had not been defoliated by herbivory within the current growing season were selected and excavated completely from each quadrat. We measured plant height (the highest stem) and counted the number of stems, bulbils and leaves. After washing, all plant samples were dried at 60 °C for 48 h, separated to stems, leaves, bulbils, roots, and rhizomes, and weighed. Individual leaves that died and remained attached to the stem base were included as part of the total dry mass. Mean stem mass, bulbil mass, and leaf mass were calculated. Seed mass was neglected because there were very few flowers in these populations. The dry mass of a plant organ relative to the total dry mass was used to indicate the relative partitioning of photo-assimilates to the particular organ on a sample date. Aboveground mass (stems, leaves and bulbils mass) and belowground mass (rhizome and roots mass) were used as measures of resources expended in organs of above- and below-ground plants. Thus the allocation to rhizome (rhizome mass: total dry mass) provides a measure of resource storage. Resource allocation to reproduction and growth were estimated by bulbils mass and by stem plus leaf mass, respectively.

We sampled species richness (SR) (in terms of the number of species per quadrat) and plant density of each species in

2001 by identifying all species present in the quadrats before measuring performance of *P. viviparum* L. var. *angustum*. We initially divided all measured species into four species groups according to Noy-Meir et al. (1989), Díaz et al. (2001) and Vesk and Westoby (2001): (i) shrubs, (ii) tall herbs (>40 cm), (iii) medium herbs (20–40 cm) and (iv) small herbs (<20 cm). We collected coverage data of each species using the point method where we divided the quadrat into a 10 × 10 grid with 100 intersecting points. We recorded all plant species that touched a point placed vertically from the grid to the ground at each of 100 intersecting points (Klein et al. 2004). We used the data to compute the summed dominance ratio (equal to relative density plus relative coverage, SDR) of each species and the Shannon-Wiener (H') diversity index. To facilitate the interpretation of H' , we took the antilog of the Shannon index ($e^{H'}$), which is the number of species that would, if each were equally common, produce the same H' as the sample (Klein et al. 2004). A complete list of species and SDR changes with grazing is given in Table 4.

Data analysis

Differences in biomass, morphological traits of *P. viviparum* L. var. *angustum* and species richness (SR), species diversity (H'), species evenness (E), and summed dominance ratio (SDR) among treatments for each year were analyzed using MANOVA (SPSS 13.0 for Windows, SPSS Inc. Chicago, IL, USA). Tukey's post-hoc tests were carried out to test the differences among means. The effects of grazing treatment on biomass allocation of *P. viviparum* L. var. *angustum* were tested with ANCOVA, with total dry mass as a covariate. Adjustments for multiple comparisons were carried out using Bonferroni correction. The treatments and blocks were used as fixed effects in both tests. All data were tested for normality and homogeneity of variance. Data transformations were considered for dry mass and stem height data (\ln), mean bulbil mass ($\ln x + 1$), number of plant parts (square root) and allocation percentages (arc sine).

To determine whether there were life history trade-offs, we calculated Pearson's correlation coefficients for growth allocation versus storage allocation, growth allocation versus reproductive allocation, reproductive allocation versus storage allocation, and bulbil numbers versus mean bulbil mass within and among treatments. In order to determine correlation among species groups' response to grazing, we conducted the Pearson's correlation analysis among the SDR of shrubs, tall herbs, medium herbs and small herbs. We conducted curve regressions using a curve estimation method for each species' SDR (Y) to grazing intensity (X) to determine the grazing response type of relative species' abundance across grazing intensity. All selected functions in the study have highest significance in an F-test through ANOVA of the curve estimation, so we could get a least value of sum of squares of dispersion between the

observation value and the prediction value, and finally get an optimal regression model for a species.

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