Grazing-Exclusion Effects on Aboveground Biomass and Water-Use Efficiency of Alpine Grasslands on the Northern Tibetan Plateau

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Abstract

The influences of grazing exclusion on plant species composition and intrinsic water-use efficiency (W_i) of alpine grasslands on the Northern Tibet Plateau are not well understood. We conducted a multisite transect field survey across the three main alpine ecosystems (meadow, steppe, and desert steppe) with nine pairs of grazing-excluded and adjacent open grazed pastures. Short-term grazing exclusion (started in 2006) did not result in significant changes in nutrients or bulk density of the surface soils (0–15 cm), but it slightly changed the aboveground biomass (AGB) and coverage at both community and species levels. Community foliar $\delta^{13}\text{C}$ and W_i differed among alpine grassland types, with values for steppe being similar to those for meadow and with desert steppe values being higher than both of these. Foliar $\delta^{13}\text{C}$ and inferred W_i differed among the dominant species and varied negatively with precipitation and positively with temperature in 2010. These results confirm that there is an environmentally selective effect on the replacement of dominant species. There was no evident difference in foliar $\delta^{13}\text{C}$ or W_i between grazing-excluded and open grazed sites, but there was a slight increase of AGB and coverage in grazing-excluded sites compared to open grazed ones at the species and community levels. These results indicated that grazing exclusion may have no clear influence on the physiological processes related to foliar water usage at the species level, but may have a cumulative effect on the carbon–water balance at the community level. Slight changes in linear regressions of foliar $\delta^{13}\text{C}$ and W_i plotted across climatic gradients indicated that grasslands under grazing management might be more sensitive to regional climatic changes.

Key Words: carbon isotope composition, Changtang Natural Reserve, grazing disturbance, pasture conservation, soil nutrients

INTRODUCTION

Estimating the influences of grazing and grazing exclusion on community structure and primary production is a common but controversial topic in grassland ecology (Belsky 1992; Guevara et al. 2001; Chen et al. 2002; Taddese et al. 2002; Loeser et al. 2007; Taddese et al. 2007). Further study of the ways in which grazing affects ecological processes could increase the accuracy of statistical models used to describe plant community responses to climate disturbance, and could improve the science used to determine grazing regulations and pasture-management systems (PMS) (Oconnor 1993; Cousins et al. 2003; Palmer et al. 2004; Tietjen and Jeltsch 2007). There is evidence that grazing exclusion could improve net primary production (NPP) and modify species composition because of

animals' selective grazing behaviors (Taddese et al. 2002; Zheng et al. 2005). However, because of the lack of evidence from long-term controlled experiments, many scientists have questioned whether positive ecological benefits could result from altered grazing regimes (Loeser et al. 2007). Alrababah and colleagues (2007) have emphasized that it is not grazing but species composition and cover parameters that affect plant diversity because of the adaptation of species to long-term grazing. Indeed, grazing could affect species richness and even α diversity in alpine grasslands at the community level (Xu et al. 2005). However, climate conditions, especially precipitation, play more critical roles in controlling soil nutrient availability and thereby regulating plant growth by influencing physiological processes related to water absorption and assimilation (Ding et al. 2007; Ma et al. 2010; Yang et al. 2010; Hu et al. 2010). However, we know much less about whether grazing exclusion interacts with climate changes to improve aboveground biomass (AGB) across the Changtang Plateau.

Water absorption and assimilation by plants are the critical physiological processes. They are closely related to the surface soil moisture in alpine habitats. Changes in soil water availability could influence nutrient cycling from soils to plants (Körner 2003). Water-use efficiency (WUE) is an indicator of the trade-off between carbon production and water transpiration (Chapin et al. 2002; Stroosnijder 2009). In recent studies, WUE estimation has been consistently viewed as a key link in carbon capture by ecosystems. Since Farquhar and colleagues

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(1989) established the algorithm for inferring intrinsic WUE (W_i) based on stable carbon isotopic composition ($\delta^{13}\text{C}$) data in plant tissues, our understanding of the adaptation mechanism of plant individuals and communities to climatic changes, such as elevated CO_2 and shifted rainfall patterns, has grown rapidly (Michener and Lajtha 2007). On the Qinghai-Tibetan Plateau, Luo et al. (2009) observed that the NPP of alpine shrubland-grassland was closely related to foliar $\delta^{13}\text{C}$. Song et al. (2008) also confirmed that the leaf $\delta^{13}\text{C}$ of dominant species reflected plant responses to environmental water gradients. However, there is still a lack of knowledge about whether grazing can modify plant WUE in Tibetan alpine grasslands at both species and community scales. Therefore, it is crucial to understand the underlying mechanism of how grazed and nongrazed alpine grasslands on the Qinghai-Tibetan Plateau respond to climate changes, especially to the shifts in patterns of precipitation at spatial and temporal scales.

This study has the following objectives: 1) to determine changes in soil nutrients, such as organic carbon, nitrogen and phosphorus, and in bulk density; 2) to examine whether grazing exclusion has significant effects on AGB and coverage at both species and community levels; 3) to determine whether foliar $\delta^{13}\text{C}$ and W_i at the species and community levels have been significantly changed by grazing exclusion; and 4) to describe changes in foliar $\delta^{13}\text{C}$ and W_i of dominant species and communities in response to spatial variations in growing-season precipitation (GSP) and growing-season temperature (GST) among grazed and grazing-excluded sites.

METHODS

Study Area, Survey Design, and Plant Samples

A field survey was performed in the experimental area of the Changtang Nature Reserve in 2010. This Reserve is located in the northwestern hinterlands of the Qinghai-Tibet Plateau and has an area of approximately 595 000 km^2 . The zonal vegetation varies westward from alpine meadow (AM, dominated by *Kobresia pygmaea*, *Kobresia humilis*, and *Cares moorcroftii*) to alpine steppe (AS, dominated by *Stipa purpurea*, *Stipa capillacea*, and *Stipa subsessiliflora* var. *basiplumosa*) to desert steppe (ADS, dominated by *S. subsessiliflora*, *Ceratoides latens*, and *Stipa glareosa*), with climate shifting from semihumid to semiarid to arid, respectively. AS dominated by *S. purpurea* is the most widely distributed vegetation type. The rainy season in a normal year begins in late May and ends in September. Approximately 85% of the yearly precipitation falls during this period. It is extremely cold all year round; the mean annual temperature (1979–2008) varies from -1.91°C to 1.25°C at our sample sites (Table 1). There is an ideal aridity gradient across the Changtang Plateau, with GSP in 2010 declining in a westward direction from 443.52 mm at the easternmost site to 140.43 mm at the westernmost sites (Table 1).

To protect the natural grassland resources, trial grazing enclosures (approximately 30–200 ha in size) have been established on the Northern Tibetan Plateau since 2006 (Shi et al. 2010). Open pastures outside these enclosures are grazed by animals of single or multiple families throughout the year or during the cold season (October to the following May). We

could not obtain enough accurate information (timing, intensity, and frequency) to describe the grazing activities that occurred in the open pastures, but the grazing intensity ranged from 0.16 sheep units $\cdot \text{ha}^{-1}$ to 2.05 sheep units $\cdot \text{ha}^{-1}$ available grassland across the Changtang Plateau.

Limited by budgets, time, and severe environments, we could not perform a multisite transect field survey at several time points to reveal effects of grazing exclusion on the community structure and ecological services of alpine grasslands in detail on the Qinghai-Tibetan Plateau. Instead, we collected data on three pairs (grazing-excluded versus open pastures) of sites in each zonal vegetation type (nine pairs in total) along the actual aridity gradient in July and mid-August 2010, although most species were in their early reproductive phase during this period (Table 1). Grazing-excluded pastures were well matched with paired adjacent open pastures, and the distance between each pair was less than 1 000 m at each site.

At each sample location, five 50×50 cm sample quadrats were arranged in a line at 20-m intervals within a plot area of 200×200 m to determine the AGB. Plants in the sample quadrat were clipped to the soil surface with scissors and sorted by species. We partitioned plant materials into foliage, stems, and flowers (fruits) in laboratory. Community foliar samples for isotope analysis were obtained with the use of a 25×25 cm metal frame nested into the middle area of the 50×50 cm sample quadrat. Foliar samples of the dominant species were extracted from species leaf materials for isotope analysis.

Soil Nutrients and Bulk Density

Five soil cores with a 3.7-cm diameter from the surface layer (0–10 cm) at each quadrat were mixed and taken to laboratory for the nutrient analysis. Meanwhile, three 100-cm^3 surface soil samples were collected at each location and kept in a mobile refrigerator during the field survey days. Upon returning to the laboratory, we placed these 100-cm^3 soil cores in an oven at 105°C for 48 h to constant weight. These samples were then weighed to 0.01 g to determine the soil bulk density (BD). Soil organic carbon (SOC) and total nitrogen (TN) were determined with the use of an MAT 253 mass spectrometer (Finnigan MAT253, Bremen, Germany) with an elemental analyzer (Finnigan, Flash EA 1112 series, Bremen, Germany). Total phosphorus (TP) was analyzed with inductively coupled plasma optical emission spectroscopy (Perkin-Elmer Optima 5300, Waltham, MA).

Stable Isotope Analysis and WUE Calculation

Representative subsamples of 3–5 g were taken from foliar samples, dried at 60°C for 48 h again, and ball-milled to a homogeneous powder. Aliquots of 2.300 ± 0.500 mg were weighed into $\Phi 3.2 \times 4$ mm tin cups (Xinda Technology Co., Ltd., Taiyuan, Shanxi, China) and combusted in an elemental analyzer (Finnigan, Flash EA 1112 series, Bremen, Germany) interfaced (ConFlo III, Finnigan MAT, Bremen, Germany) with an isotope ratio mass spectrometer (Finnigan MAT253, Bremen, Germany). In this study, carbon isotope data are presented according to the conventional formula (Equation 1):

$$\delta^{13}\text{C} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 10^3, \quad [1]$$

Table 1. Vegetation type, geographical location, and climatic conditions of the sampled sites on the Northern Tibetan Plateau.¹

Site-type	Longitude E	Latitude N	Altitude	GST	MAT	GSP	MAP
	-----°-----		--m--	-----°C-----		-----mm-----	
1-AM	91.81	31.72	4684	9.62	-1.24	430.91	493.73
2-AM	91.91	32.30	4715	9.22	-1.91	443.52	484.44
3-AM	92.03	31.68	4623	9.81	-1.05	442.26	507.66
4-AS	91.02	31.42	4582	9.32	-1.09	382.65	448.16
5-AS	90.25	31.41	4640	9.48	-0.71	346.15	401.69
6-AS	85.08	31.98	4600	11.69	0.20	253.85	212.29
7-ADS	84.05	32.29	4448	12.02	0.14	221.68	171.37
8-ADS	82.91	32.08	4477	12.58	0.90	182.15	148.00
9-ADS	81.82	32.08	4607	12.78	1.25	140.43	119.97

¹AM, alpine meadow; AS, alpine steppe; ADS, alpine desert steppe; GST, growing-season temperature; GSP, growing-season precipitation in 2010; MAT, mean annual temperature; and MAP, mean annual precipitation, 1979–2008.

where R represents the abundance ratio of $^{13}\text{C}/^{12}\text{C}$ in plant samples and the standard. Foliar samples were measured against a laboratory working standard for CO_2 gas, which was previously calibrated against IAEA-CH6 at an accuracy of $\pm 0.08\text{‰}$ SD.

Previous studies indicated that W_i could be inferred from carbon isotopic composition of plants ($\delta^{13}\text{C}_p$) if atmospheric CO_2 concentration (c_a) and isotope composition of $\delta^{13}\text{C}_a$ were known. In isotopic algorithms by Farquhar et al. (1989), the depletion of ^{13}C in photosynthetic products relative to atmosphere was termed carbon isotope discrimination ($^{13}\Delta$). This variable can be estimated from $\delta^{13}\text{C}_p$ and $\delta^{13}\text{C}_a$ with procedures specified in Equation 2. Plant physiologists have reported that $^{13}\Delta$ depends on the ratio of intercellular CO_2 concentration (c_i) to that in ambient atmosphere (c_a). This relationship can be expressed as Equation 3, where a is the fractionation of CO_2 in air (4.4‰) and b is the fractionation associated with CO_2 fixation (27‰) by plants. WUE at the leaf level is defined as the ratio of net photosynthetic rate (A) to stomatal conductance (g_s) (Equation 4), where 1.6 is the ratio of diffusivities of water vapor to CO_2 in atmosphere. Thus, many ecologists have inferred W_i from stable isotope data based on Equations 2–4 rather than the A/g_s .

$$\Delta^{13} = \frac{\delta^{13}\text{C}_a - \delta^{13}\text{C}_p}{1 + \delta^{13}\text{C}_p/1000}, \quad [2]$$

$$\Delta^{13} = a + (b - a) \frac{c_i}{c_a}, \quad [3]$$

$$W_i = \frac{A}{g_s} = \frac{c_a - c_i}{1.6} = \frac{c_a(1 - c_i/c_a)}{1.6}. \quad [4]$$

We obtained $\delta^{13}\text{C}_a$ data (−8.20‰, average of July and August) for 2010 from a long-term measuring station located at the Mauna Loa Observatory, Hawaii (lat 155°36'W, long 19°30'N, 3397 m) because there were no observations of atmospheric $\delta^{13}\text{C}_a$ over the Tibetan Plateau. The CO_2 concentration (c_a =320 ppm) on the Tibetan Plateau during the growing season of 2010 was averaged from daily data from May through August at the Damxung Flux Station (lat 91°05'E, long 30°51'N, 4300 masl) in the Tibetan alpine grasslands (Xu et al. 2007).

Growing Season Climates in 2010

Daily temperature and precipitation data for the 39 meteorological stations in the Tibet Autonomous Region from May to September 2010 were downloaded from the National Meteorological Information Centre (NMIC) of the China Meteorological Administration (CMA) and interpolated into surface products in ANUSPLIN4.3 in ArcView3.2 (ESRI, Redlands, CA) according to methods recommended by Hutchinson (Hutchinson 2004). The GST and GSP in 2010 matched with sites' locations were extracted from these meteorological raster surfaces in ArcGIS 9.2 (ESRI) for further analyses.

Statistical Methods and Data Analysis

We examined differences in mean values of soil nutrients (SOC, TN, and TP) and bulk density between grazing-excluded and open grazed pastures with the use of a paired t test at a 0.10 significance level. We examined whether grazing exclusion significantly altered coverage, biomass, foliar $\delta^{13}\text{C}$ or W_i with a two-sample t test based on our quadrat data at the community level within given vegetation types and with a paired t test based on all site means across vegetation types at a 0.10 significance level. Finally, we applied linear models to compare the sensitivity of foliar $\delta^{13}\text{C}$ and W_i responding to climate gradients at both community and species levels between grazed and grazing-excluded sites.

RESULTS

Soil Nutrients and Bulk Density

Mean soil pH varies from 6.82 for alpine meadow, to 7.27 for alpine steppe, and to 7.19 for alpine desert steppe (Table 2). Soil BD ($\text{g} \cdot \text{cm}^{-3}$) ranged from 0.96 to 1.71 and from 1.08 to 1.46 for grazing-excluded and open grazed pastures, respectively. In alpine desert steppe zone, mean total phosphorus (TP) of grazing-excluded communities was $32.9 \text{ mg} \cdot \text{kg}^{-1}$ lower than that of open grazed ones ($P=0.05$). Mean TN (%) of grazing-excluded sites versus open grazed pastures varied slightly within and across vegetation types. At the 8th paired locations, mean SOC (%) of the open grazed community (1.97) was nearly 2.6 times as that of the adjacent grazing-excluded one (0.75). Thus, in alpine desert-steppe zone, mean SOC of

Table 2. Site soil pH and comparisons of soil organic carbon (SOC, %), total nitrogen (TN, %), total phosphorus (TP, mg · kg⁻¹), and bulk density (BD, g · cm³) of surface soils (0–10 cm) between grazing-excluded and open pastures on the Northern Tibetan Plateau (paired *t* test at the 0.1 significance level; abbreviations for vegetation types to see Table 1).

Site-type ¹	pH	Grazing excluded				Open to livestock			
		SOC	TN	TP	BD	SOC	TN	TP	BD
1-AM	6.79	2.88	0.30	361.5	1.18	3.75	0.31	405.2	1.24
2-AM	6.85	1.18	0.10	214.5	0.96	1.21	0.11	205.5	1.08
3-AM	6.81	4.14	0.35	435.2	1.16	3.66	0.29	448.1	1.12
AM mean	6.82	2.73	0.25	337.1	1.10	2.87	0.24	352.9	1.15
4-AS	6.72	0.32	0.06	220.2	1.39	0.46	0.08	261.7	1.46
5-AS	7.98	1.06	0.17	365.7	1.37	1.01	0.11	288.9	1.37
6-AS	7.11	1.19	0.07	368.5	1.44	0.53	0.08	348.8	1.41
AS mean	7.27	0.86	0.10	318.1	1.40	0.67	0.09	299.8	1.41
7-ADS	7.78	0.41	0.05	333.2	1.71	0.59	0.08	379.4	1.25
8-ADS	6.63	0.75	0.12	520.8	1.30	1.97	0.13	553.9	1.44
9-ADS	7.17	0.38	0.06	622.5	1.47	0.47	0.08	642.1	1.36
ADS mean	7.19	0.51 ³	0.08 ²	492.2	1.49	1.01 ³	0.10 ²	525.1	1.35
All mean	7.09	1.37	0.14	382.5	1.33	1.52	0.14	392.6	1.30

¹AM, alpine meadow; AS, alpine steppe; and ADS, alpine desert steppe.

²Significant at the 0.10 level.

³Significant at the 0.05 level.

open grazed pastures (1.01) was nearly twice that of grazing-excluded ones (0.51).

Aboveground Biomass and Coverage

In alpine meadows, mean AGB of grazing-excluded sites (55.6 g · m⁻²) was similar to that of open grazed pastures (47.2 g · m⁻²; *P*=0.14). There was a significant difference in mean community coverage between these two site types (*P*=0.009). In alpine steppes, mean AGB of grazing-excluded sites was approximately 7.2 g · m⁻² higher than that of open pastures (*P*=0.09), and there was no significant difference in community coverage between these two site types (*P*=0.34). In alpine desert steppes, neither mean AGB nor coverage of grazing-excluded communities was significantly different from that of open grazed pastures. However, according to a paired *t* test, grazing exclusion had a positive effect on community coverage (*P*=0.018) and AGB (*P*=0.003) across zonal vegetation types on the Changtang Plateau (Table 3).

Mean AGB and coverage of dominant species in grazing-excluded sites varied from 0.69 g · m⁻² to 21.25 g · m⁻² and from 0.56% to 34.77%, respectively, whereas mean AGB and coverage of dominant-same species in open grazed pastures varied from 0.39 g · m⁻² to 17.98 g · m⁻² and from 0.52% to 25.57%, respectively, across the Changtang Plateau. Mean AGB of *K. pygmaea* C.B. Clarke was 21.25 g · m⁻² in grazing-excluded sites compared to 17.98 g · m⁻² in pastures open to livestock (*P*=0.26), with significant difference in its coverage between in grazing enclosures (34.77%) and in open pastures (25.27%) in alpine meadow zone (*P*=0.014). There was significant difference in both AGB and coverage of *S. purpurea* between in grazing-excluded sites (10.67 g · m⁻², 3.44%) and in open pastures (3.95 g · m⁻², 1.73%; *P*<0.01). Moreover, *Carex ivanovae* had a significantly higher coverage in grazing-excluded sites (2.87%) than in open ones (1.81%; *P*=0.051), as did *Festuca ovina* (4.15% vs. 1.39%; *P*=0.017).

We found that excluding grazing had no significant effect on mean AGB or coverage of dominant species other than those mentioned above (Table 4).

Stable Carbon Composition and Water-Use Efficiency

Means of foliar δ¹³C and *W_i* of grazing-excluded communities were similar to that of open pastures in both alpine meadow (*P*=0.93) and steppe (*P*=0.93) zones. However, mean foliar δ¹³C of enclosed communities without grazing was significantly lower than that of open grazed pastures in alpine desert steppes (*P*<0.01). Thus, community *W_i* of grazing-excluded pastures was 5.72 μmol C · mol⁻¹ H₂O lower than that of open pastures in alpine desert steppe zone (*P*<0.01). In general, grazing exclusion did not significantly alter foliar δ¹³C (*P*=0.24) or *W_i* (*P*=0.24) at the community level compared with the traditionally managed grazing areas (Table 3).

Most dominant species in alpine grasslands did not have a significantly different foliar δ¹³C or *W_i* in the grazing-excluded pastures from that in the open pastures. Only *Saussurea stoliczkai* (*P*=0.047), *Blysnus sinocompressus* (*P*=0.019), and *S. glareosa* (*P*=0.029) showed significant variations in foliar δ¹³C and *W_i*. For example, mean foliar δ¹³C of *S. stoliczkai* in grazing-excluded pastures was significantly more positive than that in open pastures. Thereby, the *W_i* of *S. stoliczkai* was higher (4.41 μmol C · mol⁻¹ H₂O) in the grazing-excluded pastures than that in open pastures. Foliar δ¹³C values of *B. sinocompressus* and *S. glareosa* in grazing-excluded sites were more negative than in open pastures. Thus, the *W_i* values of *B. sinocompressus* and *S. glareosa* in grazing-excluded sites were lower (6.17 and 4.16 μmol C · mol⁻¹ H₂O, respectively) than in open pastures respectively (Table 4).

Responses of Foliar δ¹³C and *W_i* to Climate Variables

Foliar δ¹³C and *W_i* significantly decreased with increasing GSP, but increased with increasing GST in grazing-excluded and

Table 3. Comparison of aboveground biomass (AGB, $\text{g} \cdot \text{m}^{-2}$), community coverage (Cover, %), foliar stable carbon isotope composition ($\delta^{13}\text{C}$, ‰), and intrinsic water use efficiency (W_i , $\mu\text{mol C} \cdot \text{mol}^{-1} \text{H}_2\text{O}$) between grazing-excluded and open pastures on the Northern Tibetan Plateau (t test based on quadrat data within a given vegetation type, paired t test based on site means across zonal vegetations).

Site type ¹	Grazing excluded				Open to livestock			
	AGB	Cover	$\delta^{13}\text{C}$	W_i	AGB	Cover	$\delta^{13}\text{C}$	W_i
1–AM	57.0	54.9	–25.65	80.48	42.4	43.9	–25.87	78.44
2–AM	68.2	70.7	–25.97	77.47	60.3	58.0	–26.1	76.30
3–AM	51.6	66.7	–25.95	77.65	38.8	43.3	–25.64	80.55
AM mean	55.6	64.1 ⁴	–25.86	78.53	47.2	51.7 ⁴	–25.87	78.43
4–AS	31.4	18	–26.13	75.98	24.9	15.8	–26.45	73.08
5–AS	34.7	13.6	–26.41	73.44	28.1	13.1	–25.91	78.06
6–AS	17.6	7.9	–25.45	82.33	9.2	4.4	–25.68	80.13
AS mean	27.9 ²	13.2	–26.00	77.25	20.7 ²	11.1	–26.01	77.09
7–ADS	8.2	11.5	–25.65	80.42	7.2	6.7	–24.76	88.64
8–ADS	11.3	12.9	–25.22	84.4	7.6	9.8	–24.40	91.99
9–ADS	7.4	9.8	–24.82	88.12	7.2	6.0	–24.67	89.46
ADS mean	8.7	8.7	–25.23 ²	84.31 ²	7.7	9.1	–24.61 ³	90.03 ³
All mean	31.9 ⁴	29.6 ³	–25.69 ⁴	80.0 ⁴	25.1 ⁴	22.3 ³	–25.50 ⁴	81.85 ⁴

¹AM, alpine meadow; AS, alpine steppe; and ADS, alpine desert steppe.

²Significant at the 0.10 level.

³Significant at the 0.05 level.

⁴Significant at the 0.01 level.

open pastures at the community and species levels (Fig. 1 and 2). The slopes of both foliar $\delta^{13}\text{C}$ and W_i responding to climate conditions in open grazed pastures were slightly steeper than those in grazing-excluded ones at the community level (Figs. 1a, 1b, 2a, and 2b). Both foliar $\delta^{13}\text{C}$ and W_i of the alpine grasslands are slightly more sensitive to temperature than to precipitation on the Changtang Plateau, and grazing exclusion could slightly improve the resistance of alpine communities to regional climate changes.

Foliar $\delta^{13}\text{C}$ and W_i of dominant species were distinctive, and few species were affected by excluding grazing (Table 4). Patterns of foliar $\delta^{13}\text{C}$ across dominant species responding to climate conditions under grazing exclusion were similar to those under grazing management (Figs. 1c and 1d). We also found that patterns of W_i responding to climate variables coincided with those of foliar $\delta^{13}\text{C}$ at the species level (Figs. 2c and 2d). Foliar $\delta^{13}\text{C}$ and W_i of dominant species declined significantly with precipitation and increased with temperature (Figs. 1c, 1d, 2c, and 2d).

Table 4. Foliar carbon isotope composition ($\delta^{13}\text{C}$, ‰) and intrinsic water-use efficiency (W_i , $\mu\text{mol C} \cdot \text{mol}^{-1} \text{H}_2\text{O}$) of dominant species in grazing-excluded and open pastures on the Northern Tibetan Plateau.

Dominant species	Grazing excluded				Open to livestock			
	AGB	Cover	$\delta^{13}\text{C}$	W_i	AGB	Cover	$\delta^{13}\text{C}$	W_i
<i>Kobresia pygmaea</i> C.B. Clarke	21.25	34.77 ¹	–26.16	75.70	17.98	25.27 ¹	–26.25	74.91
<i>Potentilla saundersiana</i> Royle	4.38	7.54	–26.80	69.84	8.60	9.37	–26.56	72.02
<i>Androsace tapeta</i> Maxim	11.27	2.82	–26.84 ¹	69.46 ¹	8.23	1.25	–27.22 ¹	65.92 ¹
<i>Potentilla bifurca</i> Linn	4.89	4.14	–26.32	74.27	8.71	7.81	–26.44	73.17
<i>Saussurea stoliczkae</i> C.B. Clarke	3.91	7.42	–27.12 ²	66.83 ²	3.61	3.57	–27.60 ²	62.42 ²
<i>Stipa purpurea</i> Griseb	10.67 ³	3.44 ³	–25.47	82.13	3.95 ^{***}	1.73 ³	–25.36	83.15
<i>Carex ivanovae</i> Egorova	7.07	2.87 ¹	–26.34	74.07	5.07	1.82 ¹	–26.29	74.51
<i>Festuca ovina</i> Linn	3.47	4.15 ²	–26.27	74.75	2.84	1.39 ²	–26.44	73.10
<i>Leontopodium nanum</i> (Hook. f. et Thoms.) Hand.-Mazz.	11.28	6.17	–27.36	64.61	8.14	3.00	–27.29	65.26
<i>Oxytropis stracheyana</i> Benth. ex Baker	2.19	1.20	–26.31	74.34	3.20	1.27	–26.18	75.58
<i>Stipa subsessiliflora</i> (Rupr.) Roshev. var. <i>basiplumosa</i> (Munro et Hook. f.) P.C. Kuo et Y.H. Sun	9.22	8.72	–25.52	81.63	4.92	5.60	–24.84	87.92
<i>Stipa glareosa</i> P. Smirn.	5.07	8.20	–25.64 ²	80.58 ²	3.38	3.00	–25.19 ²	84.74 ²
<i>Blysnus sinocompressus</i> Tang et Wang	0.69	0.56	–26.53 ²	72.31 ²	0.39	0.52	–25.86 ²	78.48 ²

¹Significant at the 0.10 level.

²Significant at the 0.05 level.

³Significant at the 0.01 level.

Figure 1. Responses of stable carbon isotope composition ($\delta^{13}\text{C}$, ‰) to growing-season precipitation (GSP) and mean air temperature (GST) between grazed (○, ---) and grazing-excluded (●, —) sites at the community (a, b) and species (c, d) levels.

DISCUSSION

Effects of Grazing Exclusion on Soil Properties and Aboveground Biomass

To the best of our knowledge, the growth and survival of plants in alpine habitats are limited by environmental conditions, including low temperatures and low nutrient availability in surface soils (Jonasson and Shaver, 1999). Surface soils can be compacted by livestock trampling, thus limiting plant growth

because of the depletion in available moisture in topsoils (Taddese et al. 2007). Soil organic carbon, available nitrogen, and phosphorus content could also be decreased by grazing activities (Dong et al. 2009; Shi et al. 2010). However, no significant change was found in soil properties in our results, including soil organic carbon, nitrogen, and phosphorus content and in bulk density.

There is increasing evidence that the aboveground biomass of alpine grasslands on the Qinghai-Tibetan Plateau is controlled primarily by precipitation (Bai et al. 2008; Hu et

Figure 2. Responses of intrinsic water-use efficiency (W_i , $\mu\text{mol C} \cdot \text{mol}^{-1} \text{H}_2\text{O}$) to growing season precipitation (GSP) and mean air temperature (GST) between grazed (○, ---) and grazing-excluded (●, —) sites at the community (a, b) and species (c, d) levels.

al. 2010; Ma et al. 2010; Yang et al. 2010). We also found that decreasing trends in the aboveground biomass and coverage of zonal alpine grassland types were both controlled by the northwestward-decreasing precipitation across the Changtang Plateau. Within a given alpine grassland type, however, there are slight improvements in community biomass and coverage of grazing-excluded sites compared with those in open grazed pastures. Previous studies have indicated that long-term grazing exclusion may not necessarily increase species richness or biomass production (Oba et al. 2001; Courtois et al. 2004; West et al. 1984). However, an optimal grazing exclusion in alpine grasslands could improve aboveground biomass at the community level (Zhou et al. 2006). It was notable that aboveground biomass and coverage of certain dominant species were higher in communities with grazing exclusion in our study. These higher values would result in changes in species dominance and compositional status. For this reason, livestock reduction and grazing exclusion are still necessary and effective measures for promoting the recovery of degraded natural grasslands (Fan et al. 2010; Wei and Chen 2001).

Effects of Grazing Exclusion on Water Usage at Species and Community Scales

The distinctive foliar $\delta^{13}\text{C}$ values among dominant species in our study indicated that dominant species might adapt to environmental changes in different ways. Responses of individuals may not scale linearly to ecosystem-level behaviors (Barbosa et al. 2010). Environmental changes may have selective effects on the replacement of dominant species. Those species would become less dominant, if water condition is unsuitable for growth, and thus would be replaced by other subdominant and more adaptable species (Song et al. 2008). Primarily species assemblage regulates foliar $\delta^{13}\text{C}$ and WUE values of communities. Moreover, species dominance (including aboveground biomass and coverage) could be changed by selective feeding behavior of animals. For example, sheep and yaks prefer grasses and sedges with good palatability rather than legumes and forbs in alpine grasslands. Our data, although not explicitly designed for all species biomass and coverage, suggest that grazing exclusion affected species composition as a result of the changed aboveground biomass and coverage of dominant species. Hence, we can conclude that in a certain time an optimal grazing exclusion would influence the water–carbon process at the community level by changing species assemblage.

Effects of Grazing Exclusion on Community Sensitivity to Climate Changes

The ecological compensation of coexisting species plays an important role in shaping the relationship between species richness and net primary production in alpine grasslands (Wang et al. 2011). Communities can respond to climate changes by altering functional characteristics of certain dominant species or by replacing dominant species with other more adaptable species (MacGillivray et al. 1995). These declining responses of both foliar $\delta^{13}\text{C}$ and W_i at the species level to growing-season precipitation and temperature confirm that dominant species in alpine grasslands co-vary with their habitat conditions and have acclimated to the disturbance caused by long-term

traditional grazing. Therefore, we did not detect any significant change in species responses to climatic variables. Another consequence is that grazing exclusion could improve the resistance of alpine grasslands to climate changes, although at the community scale both foliar $\delta^{13}\text{C}$ and WUE of grazing-excluded pastures responded to climatic variables in slightly but not significantly different ways than those pastures open to livestock.

IMPLICATIONS

Results in this study suggest that the grazing exclusion since 2006 on the Northern Tibetan Plateau has not yet changed foliar $\delta^{13}\text{C}$ of the most-dominant species, but has resulted in species compositional changes due to animals' selective feeding behavior on species individuals. Foliar $\delta^{13}\text{C}$ is species dependent, and apparent changes in foliar $\delta^{13}\text{C}$ and intrinsic WUE at the community level are primarily due to the replacement of dominant species and species compositional changes as results of grazing cessation. These findings imply that keeping species composition constant is essential to maintaining the water–carbon balance in alpine grasslands. Therefore, grazing exclusions are an effective measure for maintaining alpine grassland stability and improving resistance to potential climate changes.

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