Can Edaphic Factors Demonstrate Landscape-Scale Differences in Vegetation Responses to Grazing?
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ORIGINAL PAPER

Can edaphic factors demonstrate landscape-scale differences in vegetation responses to grazing?

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Abstract We focused on land units as landscape characteristics and selected seven typical land units on a land catena comprising two areas of southern Mongolia. Hierarchical analysis was used to test the hypothesis that a land unit's edaphic factors could explain the differences in vegetation responses to grazing. We established the survey sites at increasing distances from a livestock camp or water point within each land unit, then analysed patterns of change in floristic and functional compositions, vegetation volume and soil properties within each land unit to reveal differences in vegetation responses to grazing. We also examined the variations in floristic and functional compositions across land units to identify the edaphic factors that may underlie these differences. Changes in vegetation and soil properties at increasing distances from a camp or water point within each land unit were into three different patterns. Ordination techniques consistently indicated that land unit groups categorised using edaphic factors corresponded to those categorised using response patterns. Our study revealed that edaphic factors were responsible for the observed landscape-scale differences in vegetation responses to grazing in the study areas. In addition, the mechanisms underlying vegetation responses to grazing may have been primarily determined by edaphic factors.

Keywords Arid and semi-arid rangelands · Land degradation · Ordination · Plant functional types

Introduction

The understanding of vegetation responses to livestock grazing has become an important issue

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in rangeland management. Management that is inappropriate for a given rangeland's ecosystem may lead to the degradation of ecosystems (Briske et al. 2003). Such degradation is particularly likely in arid and semi-arid rangelands, where vegetation degradation caused by overgrazing is considered an obvious symptom of desertification, a major global environmental problem (Dregne 1986; UNEP 1992). Grazing affects arid and semi-arid ecosystems in various ways, including biomass consumption, redistribution of soil nutrients and plant seeds in urine and dung, trampling of plants, and soil compaction (Belsky and Blumenthal 1997). Hence, grazing can drive vegetation dynamics, especially in regions such as Mongolia that have a long history of grazing domestic livestock under nomadic or semi-nomadic patterns of land use.

Vegetation in arid and semi-arid rangelands has been studied extensively. Observations of vegetation responses to increasing grazing intensity report decreases (Oba et al. 2001; Fernandez-Gimenez and Allen-Diaz 2001; Riginos and Hoffman 2003; Todd 2006), increases (Fernandez-Gimenez and Allen-Diaz 2001; McIntyre and Lavorel 2001; Sasaki et al. 2005), and no change (Friedel 1981; Fensham 1998; Angell and McClaran 2001) in characteristics of the vegetation, such as cover, density, and biomass. Other studies have reported that the impact of grazing appeared as changes in the vegetation's floristic or functional composition (O'Connor and Roux 1995; Hiernaux 1998; Todd and Hoffman 1999; Sternberg et al. 2000; Landsberg et al. 2003), but a few studies have reported no such changes (Fernandez-Gimenez and Allen-Diaz 2001; Friedel et al. 2003). Thus, discussions of vegetation responses to grazing have produced no consensus.

Most studies of grazing impacts have used sites distributed within relatively small and localised landscapes. However, arid and semi-arid ecosystems are physiographically diverse and their vegetation potentially exhibits high degrees of localised adaptation. Moreover, ecological principles suggest that grazing impacts are determined by interactions with natural factors such as the vegetation, soil, and landform (Milchunas et al. 1988; Bailey et al. 1996; Adler et al. 2001). These factors may be responsible for the inconsistent results and may severely limit attempts to generalise vegetation responses to grazing on the basis of the results from one or a few sites. However, rangeland management and biological conservation are switching towards holistic management at landscape scales (*sensu* McIntyre and Hobbs 1999; Hobbs 2001).

One way to develop general (landscape-scale) rangeland management principles would be to reveal the differences in vegetation responses to grazing in different rangeland landscapes. In particular, quantification of these responses as a function of edaphic factors can help to reveal interactions between grazing and natural factors. Broad-scale studies in which grazing impacts were examined have generally shown that vegetation distributions in arid and semi-arid ecosystems are related to edaphic factors (Beever et al. 2003; Cingolani et al. 2003). For example, Cingolani et al. (2003) indicated that the magnitude of grazing-induced changes in floristic composition decreased with increasing soil moisture.

In the present study, we focused on land units as indicators of particular landscape characteristics and selected seven typical land units on a land catena at two study areas in southern Mongolia. We used hierarchical analysis to test the hypothesis that edaphic factors were responsible for differences in vegetation responses to grazing at a landscape scale.

Our objectives were to: (1) analyse changes in floristic and functional compositions and vegetation volume of a land unit's plant community to reveal differences in vegetation responses to grazing; (2) analyse the variations in floristic and functional compositions across a land unit and identify the edaphic factors that may determine the grazing impacts; and (3) discuss differences in the potential mechanisms of vegetation responses to grazing. Understanding the landscape-scale impacts of grazing on the dynamics of Mongolian rangelands will provide insights into the management of these ecosystems for biological conservation and sustainable use.

Methods

Study areas

Our study areas were in Mandalgobi (45°46′ N, 106°16′ E) and Bulgan (44°05′ N, 103°32′ E) in Mongolia's Dundgobi and South Gobi provinces, respectively. Mandalgobi and Bulgan are located in steppe and desert-steppe ecological zones, respectively. These two ecological zones cover more than half of Mongolia. The main livestock were sheep, goats, and cattle in Mandalgobi, and sheep, goats and camels in Bulgan. The kinds of livestock also differed among landscapes in these areas.

The climate is arid and cold, with a short summer. Annual rainfall averaged around 170 mm (CV = 28%) in Mandalgobi and 140 mm (26%) in Bulgan between 1993 and 2003 (Table 1). In both areas, peak rainfall occurred in July. Summer and winter temperatures averaged around 19 and –14°C in Mandalgobi, versus 21 and –11°C in Bulgan.

Survey design

To optimise sampling effort across scales, we used the frameworks of focal patch study (Brennan et al. 2002) as follows. First, denudation planes were identified by drawing summit levels on a 1:200 000 topographical map. We then selected seven typical land units from the sequence of denudation planes (i.e., a land catena): hill slope (MH), tableland (MT), pediment (MP) and depression (MD) in Mandalgobi, and upper-pediment (BUP), lower-pediment (BLP) and depression (BD) in Bulgan (Table 2). The sequence of land units on a catena ran from higher to lower topographic positions in this order in each study area. The sites (defined below) within a particular land unit were generally 10–20 km from those in another land unit; in BUP, they were 40 km from BLP. The potential vegetation type, soil texture, and the kinds of domestic livestock differed among land units. Since the Bulgan pediment was larger than the Mandalgobi pediment and had a distinct boundary between slope changes, we divided it into upper and lower land units. The land units were not selected to be statistical replicates. However, this design was originated on the hypothesis that vegetation responses to grazing are responsible for edaphic factors themselves rather than the difference of land units. Considering a sequential variation in edaphic factors among land units on a catena, we assumed that our set of land units across two study areas would work as real replicates for testing our hypothesis.

We determined the survey sites at increasing distances along grazing gradients from a livestock camp or water point within each of the seven land units to examine the grazing impacts on vegetation, using a thematic map on which all functioning camps and water points were mapped. Such grazing gradients provide an ideal examination of vegetation responses to a realistic range of long-term grazing impacts (Andrew 1988). Many rangeland studies have sampled vegetation and soils along grazing gradients from water points (Fernandez-Gimenez and Allen-Diaz 1999, 2001; Landsberg et al. 2002, 2003), human settlements or camps (Turner 1998; Riginos and Hoffman 2003) to determine the grazing impacts on rangeland structure and function. Since potential correlations between the grazing gradient and other environmental factors (especially micro-topography) often pose confounding effects of sampling

Table 1 Monthly rainfall near Mandalgobi and Bulgan (1993.2003) CV, coefficient of variation. Data provided by the Institute of Meteorology and Hydrology, Ministry of Nature and Environment

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	May to Sep	Annual
Mandalgobi														
Mean (mm)	0.9	0.8	2.3	4.9	13.5	23.4	57.4	48.9	8.6	4.1	2.6	1.4	151.8	168.8
CV (%)	142.0	137.8	48.8	115.4	101.8	36.4	68.8	50.5	91.1	146.6	92.5	107.3	31.5	28.3
Bulgan														
Mean (mm)	1.4	2.0	2.6	4.1	11.9	20.6	39.8	36.1	11.7	5.5	4.1	2.0	120.0	141.7
CV (%)	110.7	149.9	102.4	68.0	130.2	62.2	59.3	59.9	106.5	113.3	103.6	253.4	34.9	26.3

Table 2 Characteristics of each land unit and the maximum distance from a livestock camp or water point

Study area	Land unit code	Land unit	Gradient source	Potential vegetation type	Soil texture[a]	Domestic livestock grazed[b]	Maximum distance (m)
Mandalgobi	MH	Hill slope	Livestock camp	shrubland	Sand	Sheep	550
	MT	Tableland	Livestock camp	grassland	Sandy clay loam	Sheep/cattle	1150
	MP	Pediment	Livestock camp	grassland	Sandy loam	Sheep	250
	MD	Depression	Livestock camp	halophytic shrubland	Sandy loam	Sheep/camel	200
Bulgan	BUP	Upper pediment	Water point	grassland	Sandy clay loam	Goat/sheep	1500
	BLP	Lower pediment	Livestock camp	shrubland	Sand	Sheep/camel	600
	BD	Depression	Livestock camp	halophytic shrubland	Sandy loam	Camel	200

[a] Soil texture was sampled at the centre of each grazing gradient

[b] Domestic livestock was reported by the herders in each land unit

across different vegetation types and soil textures (Landsberg et al. 2002; Sasaki et al. 2005; Todd 2006), the sites where these confounding effects appeared to be minor were selected.

The maximum distance was set in each land unit (Table 2) as the distance further than the distance where the distribution of livestock's dung became scarce. The distance from each site within a land unit to a camp or water point (ln-transformed) represented grazing intensity.

Data collection

We performed field surveys in June and July 2005. Within each land unit, we sampled the vegetation and soil in "common" survey sites (3 or 4 sites for each land unit, 24 sites in total) at increasing distances from the camps or water point. Intervals of sites were different for each land unit because the vegetation and soil structure did not extend out for a uniform distance. For vegetation sampling, we established additional sites to permit robust statistical inferences about the grazing effects on vegetation within-land unit scale, and sampled five 1 × 1 m quadrats laid out every 10 m (not to be clustered) along a transect placed at the centre of each site. In each quadrat, we recorded the aerial cover (%) visually and height (cm) of each plant species. Nomenclature follows Grubov (1982).

Soil samples (6 replicated samples from the centre of common survey sites, to a depth of 5 cm) were combined for analyses of pH, electrical conductivity (EC), TN (total nitrogen), and soil organic carbon (SOC). Soil texture in each land unit (sand, silt, and clay contents based on the criteria of ISSS et al. 1994) was analysed from 6 additional samples centred within each gradient. Soil samples were air-dried and passed through a 2-mm sieve before analysis. The pH was measured with a glass electrode (soil:solution = 1:2.5, using deionised water) and the EC was measured with an EC metre (soil:solution = 1:5). TN and SOC were analysed by using dry combustion (Matejovic 1993) with decalcified soil samples to exclude carbonate carbon. All soil data are expressed on a dry-weight basis (oven-dried for 24 h at 105°C).

Data analysis

We approximated the volume occupied by each plant species in each quadrat by multiplying the cover (%) and height for the species (Ohtuka et al. 1993). After calculating the total volume for all species (hereafter, the "vegetation volume") in each quadrat, we standardised the volume of each plant species by expressing it as a proportion of the vegetation volume to represent the relative species dominance.

Plant functional types (PFTs) have been widely used to quantify the relationship between vegetation and various disturbances (e.g., Lavorel et al. 1997; McIntyre et al. 1999). In particular, PFTs have been used to examine the relationship between vegetation and grazing in arid and semi-arid areas; previous rangeland studies have suggested that community responses to grazing are strongly associated with plant life-form and palatability to livestock (e.g., Fernandez-Gimenez and Allen-Diaz 2001; McIntyre and Lavorel 2001; Jauffret and Lavorel 2003). We therefore classified the plant species found in the survey into PFTs defined as a combination of life form, relative palatability to livestock, and sensitivity to salinity: palatable, unpalatable, or halophytic shrubs; palatable, moderately palatable, or unpalatable perennial herbs (hereafter, perennials); and annual herbs (generally unpalatable, hereafter, annuals). Relative palatability was determined from the information provided by Jigjidsuren and Johnson (2003).

Our numerical analyses focused on changes in floristic and functional compositions according to environmental gradients, including grazing intensity. Two kinds of data sets, which differed in terms of data resolution, were prepared: (1) seven data matrices comprising the floristic and functional compositions in each quadrat within each land unit, and (2) a data matrix of floristic and functional compositions at each common survey site across land units (species volumes in each quadrat were pooled within each common site and standardised to a relative value as defined above). Before each analysis, floristic and functional compositions data were $\log_{10}$-transformed. To test our hypothesis, we used the following hierarchical analytical approach:

Step 1. Analyses of vegetation responses to grazing within each land unit

First, we attempted to reveal differences in vegetation responses to grazing among land units. Data for the individual quadrats within each land unit were subjected to two-way indicator species analysis (TWINSPAN; Hill 1979b) using PC-ORD for Windows (version 3.0, McCune and Mefford 1997). TWINSPAN analyses were generally used to classify the vegetation samples on the basis of compositional similarity, but TWINSPAN can also be used to divide an ordination space for several types of ecological data (McCune and Mefford 1997). On the basis of the results, individual quadrats were classified into community types within each land unit. We then performed indicator-species analysis (INSPAN; Dufrene and Legendre 1997) for each community type. INSPAN outputs reveal indicator species that have a strong and significant association with a given community type (indicator value > 25, $P < 0.05$).

We also performed detrended correspondence analysis (DCA; Hill 1979a) for the floristic and functional compositions of the individual quadrats within each land unit, and then explored the relationships between DCA axes (interpreted as a grazing indicator) and distances by means of linear regression. We also explored the relationship between soil parameters (TN, SOC, EC and pH) and distances by means of linear regression.

To analyse the relationship between grazing intensity and vegetation volume, we fitted the vegetation volume data in individual quadrats within each land unit against the distance as the explanatory variable using generalised linear models (GLM; McCullagh and Nelder 1989). Vegetation volume has a large variance for the mean value for all quadrats within a land unit and may thus have a Gamma distribution; thus, the GLM used a logarithmic link function.

Step 2. Analyses of vegetation distribution across land units and identification of edaphic factors that may explain differences in vegetation responses to grazing

A preliminary DCA for the floristic and functional compositions of each common sampling site across land units showed that the main environmental gradients in the data were 16.7 and 3.7 standard deviation units (Gauch 1982), respectively. We therefore used canonical correspondence analysis (CCA; ter Braak 1986), but implemented following the approach of Legendre and Legendre (1998) for floristic composition, and redundancy analysis (RDA; Legendre and Legendre 1998) for functional composition. After testing for collinearity, the overall variances of floristic and functional compositions were analysed by means of CCA and RDA using all soil variables, which were averaged by each site or gradient (pH, EC, SOC, TN, and the sand, silt, and clay contents, ln-transformed distance from the camp or water point). We used permutation tests (100 permutations) to test the significance of the first axis eigenvalue (Legendre and Legendre 1998).

From the results of the CCA and RDA ordinations, we delimited land unit groups that corresponded to particular edaphic factors in the ordination space, then examined whether these edaphic factors could explain the landscape-scale differences in vegetation responses to grazing.

All statistical analyses (except for TWINSPAN and INSPAN) were performed with R software (version 2.1.1, R Development Core Team 2005).

Results

Differences in vegetation responses to grazing

We found 63 plant species across seven land units. Community types in each land unit were determined using TWINSPAN. Each community type was numbered in order of its proximity to the camp or water point. Combining the results from TWINSPAN and INSPAN (data are not shown) with the results of the DCA ordination, regression analyses, and GLM revealed that the vegetation responses to grazing could be categorised into three patterns:

Patterns of changes in vegetation and in soil properties according to grazing intensities in MH and BLP were similar as follows. Changes in floristic composition appeared along axis 1 (BLP) or axis 2 (MH) of the DCA ordination (Fig. 1a and f). In BLP, changes in functional composition appeared along axis 1 of the DCA ordination (Fig. 2f), but there were no distinct changes along either axis in MH (Fig. 2a). Regression analyses (Table 3) indicated that variations in floristic composition in both land units were significantly associated with distance. Variations in functional composition were also associated with distance in BLP, but not in MH. SOC and soil pH decreased with decreasing distance (i.e., with increasing grazing intensity) in MH. In BLP, TN, SOC, and EC increased with decreasing distance. Although changes in soil parameters differed to a greater or lesser degree, the magnitude of the R^2 value (lower than for other land units) showed that these soil environmental variables were not strongly related to the distance. In BLP, the positions of indicator species and PFTs in the DCA ordination spaces for the floristic and functional compositions indicated that an unpalatable shrub (*Brachanthemum gobicum*, the indicator species for BLP1; Bg in the ordination space) was noted at the left extreme of axis 1 (decreasing distance, i.e., high grazing intensity) and the palatable shrub *Caragana korshinskii* (for BLP3, Ck in the ordination space) was noted at the right extreme of axis 1 (i.e., at low grazing intensity). In MH, there were no changes in the shrub layer but there were changes in the herb layer; the unpalatable perennial *Potentilla bifurca* (for MH1, Pb) was noted at the top of axis 2 (decreasing distance, i.e., high grazing intensity) and palatable perennials such as *Stipa krylovii* (for MH4, Sk) and *Agropyron cristatum* (for MH4, Acr) were noted in the lower extreme of axis 2 (i.e., low grazing intensity). Thus, floristic composition changed to a greater or lesser extent in MH but without a corresponding change in functional composition. In both land units, GLM results (Fig. 3a and f) showed that vegetation volume decreased with decreasing distance.

Patterns of changes in vegetation and in soil properties according to grazing intensities in MT, MP, and BUP were similar as follows. Changes in floristic composition (Fig. 1b, c and e) and functional composition (Fig. 2b, c and e) appeared along axis 1 of the DCA ordination. Regression analyses (Table 3) indicated that the variations in floristic and functional compositions were significantly associated with the distance. Except for pH, which was only significantly correlated with distance in MT, values of all soil environmental variables increased with decreasing distance. The positions of indicator species and PFTs in the DCA ordination spaces for floristic and functional compositions consistently indicated that unpalatable perennials and annuals such as *Peganum nigellastrum* (indicator species for MT2 and BUP1, Pn) and *Chenopodium album* (for MT1, MP1 and BUP1, Cal) were noted towards the right end of axis 1 (increasing TN, SOC and EC, and decreasing distance, i.e., high grazing intensity). Toward the left end of this axis (i.e., low grazing intensity), palatable perennials such as *Stipa* spp. (for MT3, MP3 and BUP4, Sk, Sgl, and Sgo), *Allium* spp. (for MT3 or MT4, MP3, and BUP4, Aan and Ap), and *Carex* spp. (for MT3, MP3 and BUP3, Cdu and Cst) appeared. In all land units, GLM results (Fig. 3b, c and e) showed that vegetation volume increased as distance decreased.

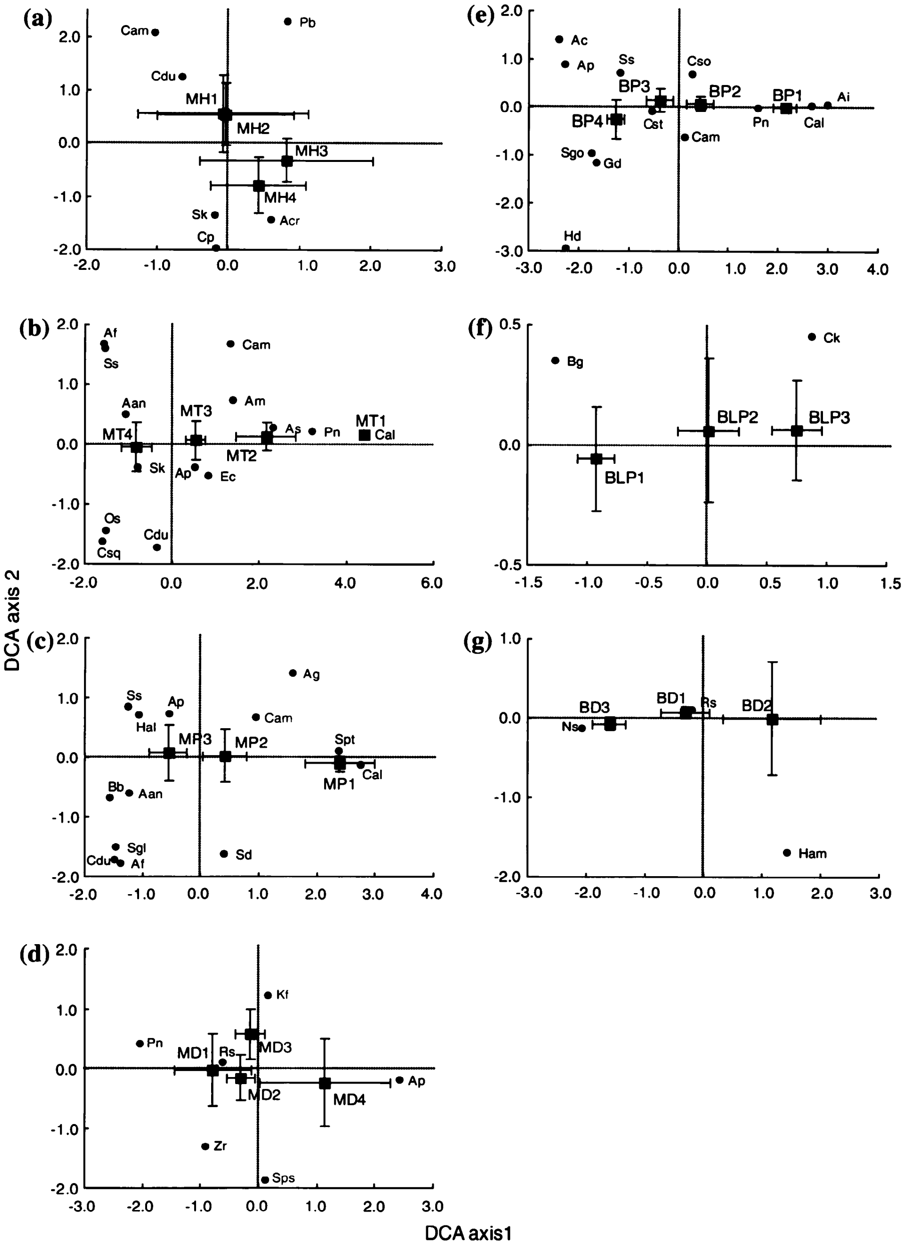


Fig. 1 Biplots of the DCA of floristic composition of quadrats within each land unit. (**a**) MH; (**b**) MT; (**c**) MP; (**d**) MD; (**e**) BUP; (**f**) BLP; (**g**) BD. Centroids (±SD) of the individual quadrats categorised by each community type (classified using TWINSPAN) are indicated (■); Indicator species for each community type are also marked (•); Abbreviations of nomenclature: Aan, Allium anisopodium; Ac, Artemisia caespitosa; Acr, Agropyron cristatum; Af, Artemisia frigida; Ag, Asparagus gobicus; Ai, Achnatherum inebrians; Am, Allium mongolicum; Ap, Allium polyrrhizum; As, Achnatherum splendens; Bb, Bupreurum bicaule; Bg, Brachanthemum gobicum; Cal, Chenopodium album; Cam, Convolvulus ammanii; Cdu, Carex duriuscula; Ck, Caragana korshinskii; Cp, Caragana pygmaea; Cso, Cleistogenes songorica; Csq, Cleistogenes squarrosa; Cst, Carex stenophylloides; Ec, Elymus chinensis; Gd, Gypsophila desertorum; Hal, Heteropappus altaicus; Ham, Haloxylon ammodendron; Hd, Haplophyllum dauricum; Kf, Kalidium foliatum; Ns, Nitraria sibirica; Os, Orostachys spinosa; Pb, Potentilla bifurca; Pn, Peganum nigellastrum; Sd Scorzonera divaricata; Sgl, Stipa glareosa; Sgo, Stipa gobica; Sk, Stipa krylovii; Sps, Salsola pesserina; Spt, Salsola pestifera; Ss, Sibbaldianthe sericea; Rs, Reaumuria soongorica; Zr, Zygophylum rosovii

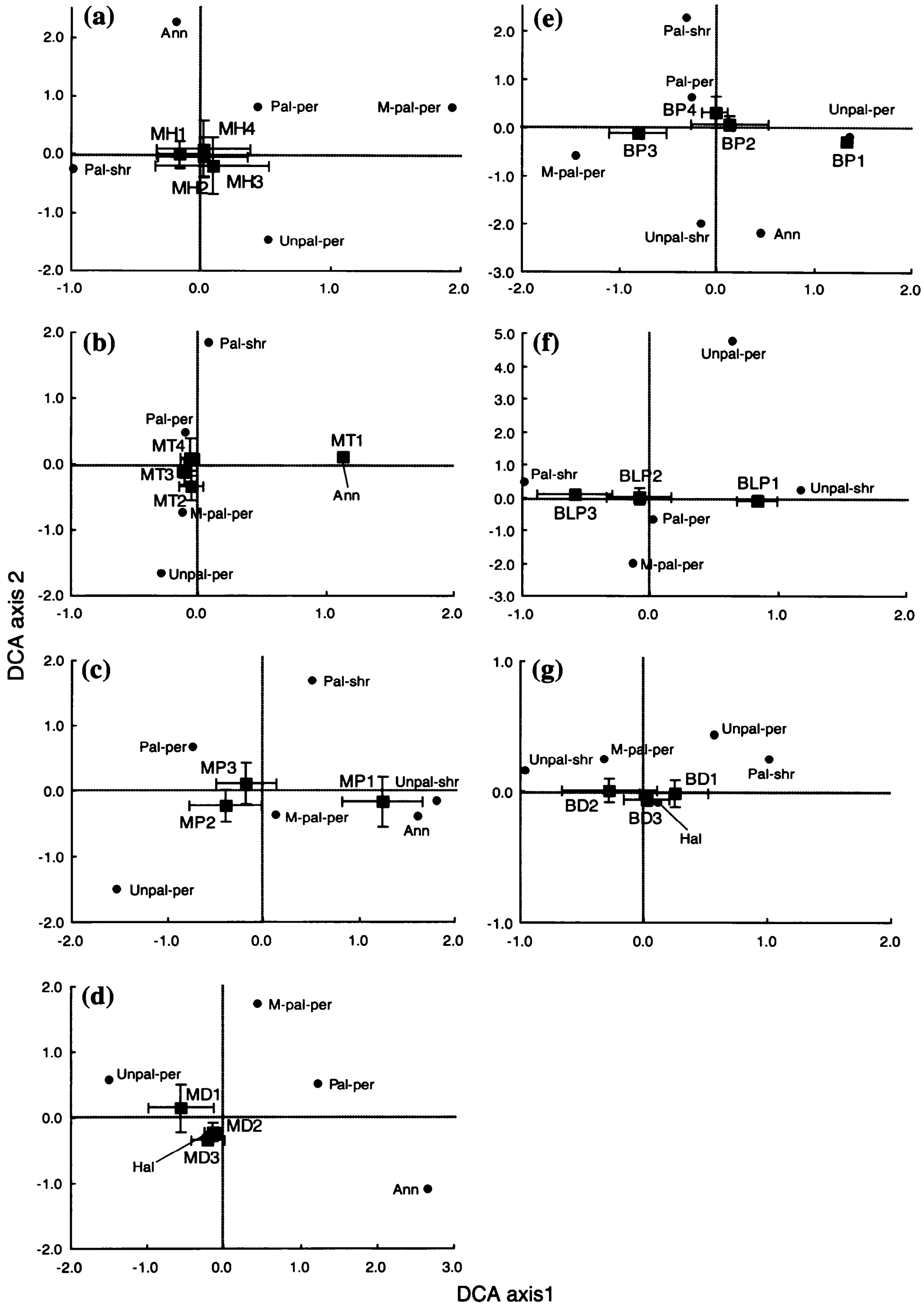
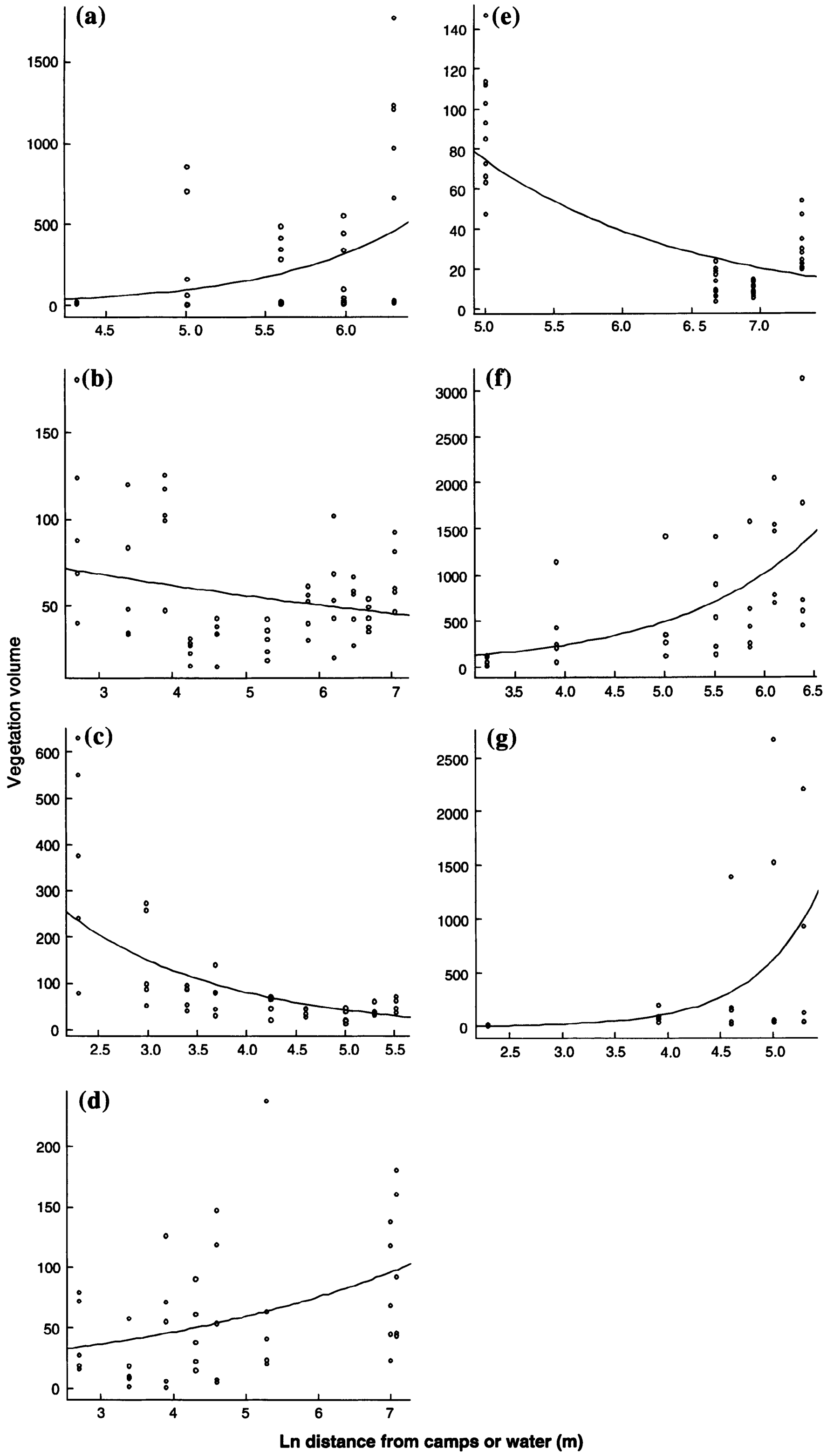


Fig. 2 Biplots of the DCA of functional composition of quadrats within each land unit. (**a**) MH; (**b**) MT; (**c**) MP; (**d**) MD; (**e**) BUP; (**f**) BLP; (**g**) BD. Centroids (±SD) of the individual quadrats categorised by each community type (classified using TWINSPAN) are indicated (■); Plant functional types are also marked (●); Plant functional types: Pal-shr, palatable shrubs; Unpal-shr, unpalatable shrubs; Pal-per, palatable perennials; M-pal-per, moderately palatable perennials; Unpal-per, unpalatable perennials; Ann, annuals (generally unpalatable); Hal, halophytic shrubs

Table 3 Summary of regression analyses relating the distance to the DCA axis scores for floristic and functional compositions, TN, SOC, EC and pH. Scores of DCA axis 1 for both floristic and functional compositions, which can be interpreted as a grazing indicator, were generally used for the analyses; in MH, the scores of DCA axis 2 for floristic composition were used. Bold values indicate significant relationships ($P < 0.05$)

Land unit	DCA axes scores (floristic composition)				DCA axes scores (functional composition)				TN			
	Coefficient	Intercept	R^2	P	Coefficient	Intercept	R^2	P	Coefficient	Intercept	R^2	P
MH	-0.677	3.839	0.278	**<0.001**	0.168	-1.030	0.028	0.271	0.010	0.013	0.111	0.111
MT	-1.112	6.082	0.772	**<0.001**	-0.139	0.756	0.298	**<0.001**	-0.122	0.394	0.637	**<0.001**
MP	-1.069	4.771	0.793	**<0.001**	-0.423	1.834	0.382	**<0.001**	-0.076	0.242	0.581	**<0.001**
MD	0.266	-1.139	0.067	0.167	0.167	-0.748	0.064	0.177	-0.045	0.115	0.674	**<0.001**
BUP	-1.396	9.249	0.928	**<0.001**	-0.767	5.091	0.670	**<0.001**	-0.059	0.249	0.891	**<0.001**
BLP	0.217	-1.159	0.12	**0.048**	-0.208	1.093	0.139	**0.033**	-0.008	0.035	0.425	**0.001**
BD	0.241	-1.027	0.053	0.292	-0.069	0.337	0.030	0.429	-0.027	0.068	0.803	**<0.001**
	SOC				EC				pH			
	Coefficient	Intercept	R^2	P	Coefficient	Intercept	R^2	P	Coefficient	Intercept	R^2	P
	0.169	-0.050	0.167	**0.048**	-0.042	-1.030	0.028	0.271	0.421	5.504	0.168	0.047
	-1.342	4.161	0.713	**<0.001**	-0.106	0.756	0.298	**<0.001**	-0.817	9.708	0.678	**<0.001**
	-1.325	3.330	0.800	**<0.001**	-0.232	1.834	0.382	**<0.001**	0.026	7.378	0.002	0.866
	-0.428	1.020	0.652	**<0.001**	0.001	-0.748	0.064	0.177	0.905	7.182	0.214	0.053
	-0.632	2.517	0.914	**<0.001**	-0.081	5.091	0.670	**<0.001**	0.210	7.695	0.323	0.054
	-0.044	0.173	0.226	**0.019**	-0.018	1.093	0.139	**0.033**	-0.065	9.243	0.048	0.305
	-0.338	0.752	0.781	**<0.001**	-0.121	0.337	0.030	0.429	-0.070	9.701	0.046	0.393

Fig. 3 The relationships between vegetation volume and distance illustrated by GLM ($P < 0.05$). (**a**) MH; (**b**) MT; (**c**) MP; (**d**) MD; (**e**) BUP; (**f**) BLP; (**g**) BD. The distance (m) was ln-transformed. Vegetation volume was calculated by multiplying the cover (%) and maximum height (cm) for each species and summing these values for all species



Patterns of changes in vegetation and in soil properties according to grazing intensities in MD and BD were similar as follows. Changes in floristic composition (Fig. 1d and g) and functional composition (Fig. 2d and g) did not appear along both axes of the DCA ordination. Regression analyses (Table 3) indicated that variations in floristic and functional compositions were unrelated to distance. Of the soil parameters, TN and SOC increased with decreasing distance in MD. In BD, TN, SOC, and EC increased with decreasing distance. In MD, the positions of indicator species in the DCA ordination space for floristic composition indicated that the unpalatable perennial *P. nigellastrum* (indicator species for MD1, Pn) occurred at the left end of axis 1, whereas a palatable perennial (*Allium polyrrhizum*; for MD4, Ap) occurred at the right end; however halophytic shrubs such as *Reaumuria soongorica* (for MD2, Rs) and *Kalidium foliatum* (for MD3, Kf) occurred near the middle. In BD, halophytic shrubs such as *R. soongorica* (for BD1, Rs) occurred near the middle of axis 1, *Nitraria sibirica* (for BD3, Ns) occurred near the left end, and the palatable shrub *Haloxylon ammodendron* (BD2, Ham) occurred in the lower-right quadrant. DCAs for functional composition in MD and BD showed centroids of individual quadrats for each community type clustered in the centre of the space, where the halophytic shrubs occurred. We therefore could not identify variations in species appearance according to grazing intensities. In MD and BD, GLM results (Fig. 3d and g) showed that vegetation volume decreased with decreasing distance.

Edaphic factors responsible for differences in vegetation responses to grazing

We performed CCA and RDA ordinations for variations in the floristic and functional compositions of each common survey site (data from individual quadrats were pooled) across land units to identify the edaphic factors that may have been responsible for the differences in vegetation responses to grazing (Figs. 4 and 5; Table 4).

In the CCA ordination (Fig. 4, Table 4), a permutation test indicated that the eigenvalue for axis 1 was significant ($P < 0.05$). Axis 1, which explained 10.9% of the variance, shows a gradient of increasing pH, EC and sand content, and decreasing distance, SOC, TN, and silt and clay contents. Axis 2, which explains 10.3% of the variance, shows a gradient of increasing distance and sand content, and decreasing SOC, TN, EC, and silt and clay contents. Axis 3 explains an additional 9.8% of the variance. The CCA ordination identified the edaphic factors influencing variation in vegetation across land units: *C. korshinskii* (Ck) and *Caragana microphylla* (Cm) appeared in the upper quadrants and represent the cluster of sites in MH and BLP; these land units were associated with increasing sand content. *Allium anisopodium* (Aan), and *A. polyrrhizum* (Ap), appeared in the lower left quadrant, which represents the cluster of the sites in MT, MP, and BUP; these land units were associated with increasing TN, SOC, and silt and clay contents. *Reaumuria soongorica* (Rs) and *K. foliatum* (Kf) appeared in the lower right quadrant, which represents the cluster of sites in MD and BD; these land units were associated with increasing pH and EC. Although distance was strongly and positively correlated with axis 2, we could not exactly identify how each common survey site corresponded to distance.

Since the relative importance of the soil variables differed among functional types, we examined variations in functional composition across land units using RDA (Fig. 5, Table 4). In the RDA ordination, the permutation test indicated that the eigenvalue for axis 1 was significant ($P < 0.05$). Axis 1, which explained 32.6% of the variance, shows a marked gradient of increasing pH, EC and sand content, and decreasing distance. Axis 2, which explained 22.8% of the variance, shows a marked gradient of increasing sand content, and decreasing TN, SOC and silt content. The RDA ordination of functional composition also identified the edaphic factors influencing the variation in vegetation across land units: palatable or unpalatable shrubs in the cluster of sites in MH and BLP were associated with increasing sand content; all perennials and annuals in the cluster of sites in MT, MP and BUP were associated with increasing TN, SOC and silt content; and halophytic shrubs in the cluster of

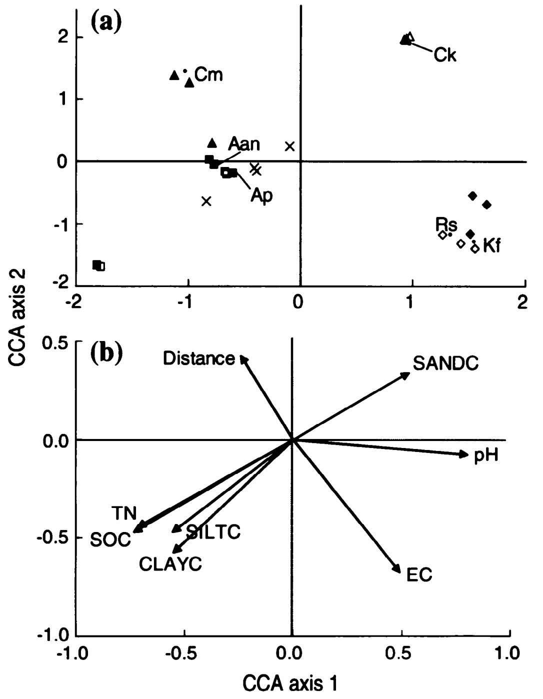


Fig. 4 CCA biplots for (**a**) floristic composition of common survey sites and (**b**) environmental vectors. Only dominant species in each land unit are plotted. Nomenclature abbreviations are described in the text. MH (▲), MT (■), MP (□), MD (◇), BUP (×), BLP (Δ), and BD (♦)

sites in MD and BD were associated with increasing pH, EC and silt content. Although distance was strongly and negatively correlated with axis 1, we could not identify well how each common survey site corresponded to distance.

Consequently, both ordination techniques (CCA and RDA) indicated that land unit groups categorised using edaphic factors corresponded to those categorised using response patterns. Our hypothesis that edaphic factors can explain landscape-scale differences in vegetation responses to grazing was clearly supported by the results.

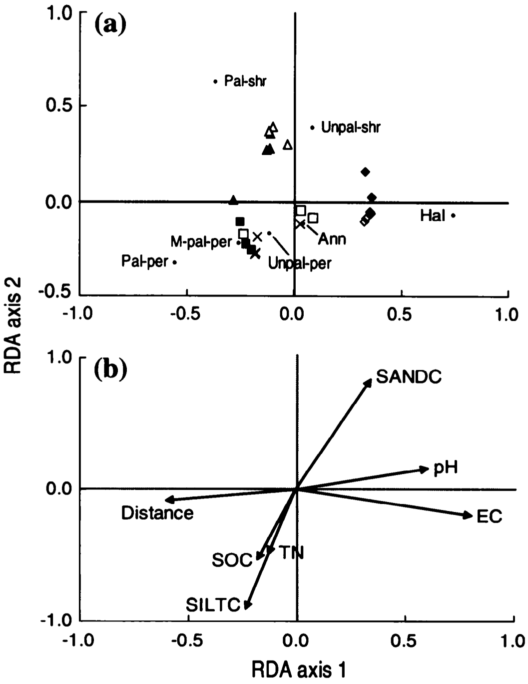


Fig. 5 RDA biplots for (**a**) functional composition of common survey sites and (**b**) environmental vectors. MH (▲), MT (■), MP (□), MD (◇), BUP (×), BLP (Δ), and BD (♦). Plant functional types are marked (•). Plant functional types: Pal-shr, palatable shrubs; Unpal-shr, unpalatable shrubs; Pal-per, palatable perennials; M-pal-per, moderately palatable perennials; Unpal-per, unpalatable perennials; Ann, annuals (generally unpalatable); Hal, halophytic shrubs

Discussion

We found that vegetation responses to grazing differed greatly among land units (Figs. 1 to 3; Table 3). The CCA and RDA ordinations (Figs. 4 and 5; Table 4) indicate that the edaphic factors characterising a particular land unit could by themselves explain most of the observed differences. This finding was true for both study areas even though annual rainfall is lower in Bulgan (Table 1), suggesting that edaphic factors may have had more influence on the vegetation responses to grazing than differences in potential climatic factors. Our hierarchical analysis provided a valid test of our hypothesis because it demonstrated that distance from camps or water points provided a strong but indirect measure of grazing intensity, thereby avoiding the need to directly measure grazing intensity and livestock density, which are two factors that might not be well derived using CCA or RDA across broader scales.

Potential mechanisms responsible for vegetation responses to grazing in sandy soils

MH and BLP are dominated by sandy soils, which were responsible for the dominance of shrubs.

Table 4 Summary of the canonical correspondence analysis (CCA) for floristic composition of common survey sites, and redundancy analysis (RDA) for functional composition of common survey sites

Axis	CCA			RDA		
	1	2	3	1	2	3
Eigenvalue	0.926	0.876	0.837	1.084	0.758	0.453
Species–enviroment correlations	0.988	0.982	0.955	0.923	0.956	0.961
Cumulative variance (%) of species data	10.870	21.150	30.980	32.590	55.380	68.990
Biplot scores for environmental variables						
Distance	−0.254	0.435	0.410	−0.613	−0.091	−0.442
SOC	−0.725	−0.461	−0.378	−0.174	−0.535	0.740
TN	−0.723	−0.445	−0.413	−0.126	−0.493	0.811
pH	0.818	−0.074	−0.285	0.608	0.161	−0.283
EC	0.513	−0.675	−0.386	0.806	−0.209	0.148
SANDC	0.548	0.348	−0.156	0.346	0.846	−0.135
SILTC	−0.562	−0.483	0.206	−0.231	−0.913	0.174
CLAYC	−0.556	−0.577	0.258	—†	—	—

SOC, soil organic carbon (%); TN, total nitrogen (%); pH, soil pH (H_2O); EC, electrical conductivity (μS cm^{-1}); SANDC, sand content (%); SILTC, silt content (%); CLAYC, clay content (%); †, The variable was excluded because of collinearity

Since floristic composition varied according to grazing intensities in both land units, and functional composition also varied in BLP, the impacts of grazing on vegetation were clear. The shifts in functional composition in BLP were consistent with the results of Riginos and Hoffman (2003). The decrease in vegetation volume with increasing grazing intensity resulted from a decrease in palatable shrubs (dominant in most community types) as a result of grazing and trampling.

The changes in TN and SOC in MH and BLP were smaller. However, N and C concentrations were greater near livestock camps or water points in other studies (Tolsma et al. 1987; Turner 1998). The redistribution of nutrients near camps or water points probably occurs by concentration of livestock urine or dung. Since sandy landscapes are highly erodible (Hennessy et al. 1986), N and C may be dispersed by wind erosion. Furthermore, replacement of palatable vegetation by unpalatable perennials or annuals under heavy grazing may possibly be retarded by positive feedback between decreasing vegetation volume and increasing wind erosion, such as wind erosion that fractures the vegetation cover (Armbrust and Retta 2000; Bielders et al. 2001) and vegetation that plays an important role in protecting topsoil against wind erosion (Bilbro and Fryrear 1994; Dong et al. 2001). In this context, it is likely that the difference in the magnitude of the positive feedback cause differences in the changes in functional composition; replacement of palatable vegetation by unpalatable shrubs under heavy grazing was found in BLP, but not in MH. Similarly, SOC decreased somewhat as grazing intensity increased in MH, but increased slightly in BLP (i.e., the positive feedback was stronger in MH). Since this is indirect evidence for differences in the magnitude of the positive feedback (initially, due to wind erosion), the cause of the observed differences in the mechanisms responsible for vegetation responses in MH and BLP remains unclear. However, our comparison across land units suggests that land degradation may closely be associated with wind erosion at these land units.

Potential mechanisms responsible for vegetation responses to grazing in sandy loam or sandy clay loam soils

MT, MP and BUP were dominated by sandy loams or sandy clay loams (i.e., relatively fine soil texture), and this was responsible for the dominance of herbs. Floristic and functional compositions varied distinctly according to grazing intensities. Analyses of the shifts in floristic and functional compositions consistently showed that a plant community dominated by palatable perennials shifted to a plant community dominated by unpalatable perennials or annuals as grazing intensity increased. These shifts were consistent with those in other studies (e.g., Sternberg et al. 2000; McIntyre and Lavorel 2001; Jauffret and Lavorel 2003). Grazing impacts associated with livestock foraging based on palatability were reflected in the vegetation responses. All soil variables except pH increased with decreasing grazing intensity. Grazing impacts may also have influenced plant community composition indirectly, by the redistribution of nutrients near camps or water points due to the concentration of urine and dung and the increase in the quantity of plant litter associated with increased vegetation volume. Fernandez-Gimenez and Allen-Diaz (2001) also predicted this effect, and we observed direct evidence of this phenomenon; the quantity of dung increased exponentially with increasing proximity to a camp or water point in these land units (T. Okayasu, unpublished data). Compared with MH and BLP, soil erodibility by wind may be lower in MT, MP and BUP, and so unpalatable perennials and annuals such as *P. nigellastrum* and *C. album* became more abundant in heavily grazed sites. In addition, the increasing vegetation volumes with increasing grazing intensity coincided with the replacement of palatable species by these unpalatable species. Consequently, our results indicated that in MT, MP and BUP grazing impacts might determine the community structure without interactions with abiotic factors such as wind erosion. This is likely to be linked to the potential mechanisms of land degradation at these land units.

Potential mechanisms responsible for vegetation responses to grazing in salinised soils

In MD and BD, the prominence of salinised soils (with higher pH and EC) determined the dominance of halophytic shrubs. We found no significant variations in floristic and functional compositions according to grazing intensities. Despite the dominance of halophytic shrubs (generally unpalatable) in MD and BD, the vegetation volume decreased as grazing intensity increased. Trampling by large livestock such as camels may have caused the decreased vegetation volume. Friedel et al. (2003) also reported a decrease in the density of unpalatable shrubs with increasing grazing intensity, mainly because of trampling by cattle. Consequently, the impacts of grazing appeared as changes in vegetation quantity rather than compositional changes. The impacts of grazing may therefore be overwhelmed by edaphic factors (particularly pH and EC) in MD and BD.

Conclusions

Although the results should not be broadly generalised because we studied only a limited number of rangeland ecosystems, our findings can nonetheless contribute to sustainable management of the study areas and can provide insights into rangeland ecology elsewhere. Our study revealed that edaphic factors were responsible for the observed landscape-scale differences in vegetation responses to grazing in the study areas. In addition, the mechanisms underlying vegetation responses to grazing may have been primarily determined by edaphic factors. The impacts of concentrated grazing on vegetation dynamics could generally lead to marked reductions in forage resources (except in salinised landscapes), and land degradation caused by grazing might be related to abiotic factors such as wind erosion, especially in sandy landscapes. The approach used in our study will be useful in understanding other rangeland ecosystems at a landscape-scale using a variety of vegetation parameters.

A limitation of our study was that due to the correlation of grazing gradients with soil parameters measured, we could not distinguish the direct effects of gradient in livestock densities with distance from camps or a water point on plant community composition through foraging based on palatability from the indirect effects caused by increasing the relative concentrations of certain nutrients in the vicinity of camps or a water point. More controlled studies of the impacts of different grazing intensities as well as grazing removal are needed to better examine these mechanisms and vegetation responses to grazing in Mongolian rangelands.

Furthermore, our study provided insights into variations in floristic and functional compositions related to grazing intensities that could be used as benchmarks of the boundary between optimal states and transition to worse states. Such response types have been proposed as key elements in a state-and-transition model (Westoby et al. 1989) of vegetation dynamics in the context of grazing impacts and edaphic stresses. On the other hand, we could not precisely define the non-equilibrium characteristics (Ellis and Swift 1988) of the observed changes in floristic and functional compositions. Whether non-equilibrium characteristics exist in the study areas remains unclear, because we could not examine the annual variability in vegetation using the present data. Ellis (1995) predicted that non-equilibrium dynamics are likely to occur where the coefficient of variation in annual rainfall is high (33%) and mean annual rainfall is low (<250 mm). Since the interannual climatic variability was high in the two study areas (see Table 1), vegetation in these areas may exhibit both equilibrium and non-equilibrium characteristics. Long-term observations are therefore needed to more definitively examine the impact of grazing and abiotic factors such as edaphic factors and interannual rainfall variability that drive vegetation dynamics in Mongolian rangelands.

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