



Vegetation change along gradients from water sources in three grazed Mongolian ecosystems

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Abstract

Foliar cover of plant species; grass, forb and total herbaceous biomass; soil P, K, N and C; and percent coarse fraction of soils were sampled over two years along grazing gradients from livestock water sources in three grazed Mongolian steppe ecosystems of varying productivity. Samples within each of the three systems (mountain-steppe, and desert-steppe) were classified into plant communities using TWINSpan and species-environment relationships in each system were examined using CCA. Community classifications were driven by the presence/absence of ruderal species and highly palatable grasses in the steppe and mountain-steppe and by the presence/absence of salt-shrub or *Caragana* shrub species and associated *Iris* species in the desert-steppe. Ordinations were largely driven by soil nutrient concentrations, particularly P and K, in all three zones. Bulk density and percent coarse fraction to 10 cm were also important in the desert-steppe. Distance from water, which we assumed to be inversely related to grazing pressure, was a significant driving factor in steppe and mountain-steppe ordinations, and was negatively correlated with P and K. We speculate that elevated nutrient concentrations near water sources result from livestock redistributing nutrients in the landscape by voiding urine and feces in the areas where they congregate. Livestock may thus influence species composition in these systems both through the direct effects of defoliation and trampling, and the indirect effects of nutrient enrichment and depletion over the broader landscape. This hypothesis deserves further testing under controlled conditions.

Introduction

The steppe grasslands of Mongolia comprise one of the largest undeveloped grassland ecosystem complexes of the world. Over 70% of Mongolia's 1.5 million square kilometers falls into three major ecological zones: the desert-steppe, steppe and mountain-steppe. These grasslands support most of Mongolia's 30 million head of domestic livestock (camels, cattle, yaks, horses, sheep and goats) as well as populations of wild ungulates, including two species of gazelle (*Gazella subgutturosa* and *Procarpa gutturosa*), argali (*Ovis ammon*), ibex (*Capra sibirica*), wild bactrian camel (*Camelus ferus*), wild ass (*Equus hemionus*), the saiga antelope (*Saiga tatarica*), and reintro-

duced populations of Przewalski's horse (*Equus przewalskii*).

Despite the ecological, conservation and economic significance of Mongolia's grasslands (extensive livestock production accounts for over 30% of Mongolia's gross domestic product), relatively little is known about the vegetation composition and dynamics of these ecosystems. Of the three national-scale classifications of Mongolia's vegetation (Hilbig 1995; Ulziikhutag 1989; Yunatov 1977), only Hilbig (1995) is in English and readily available to an international audience. Two other classifications focussing on mountain-steppe and forest-steppe vegetation have been published in English (Pacyna 1986; Wallis de Vries et al. 1996). Most of these studies employ

Braun-Blaunquet phytosociological methodology. We were unable to locate any published quantitative classifications or ordinations of Mongolian vegetation.

Few scientific data are available on the response of Mongolian grassland vegetation to increasing grazing intensity or the removal grazing (Chogni 1989; Lhagvajav 1992; Tserendash and Erdenebaatar 1993; Tsogoo 1990). These studies all were conducted in the mountain-steppe and steppe zones. We found no field studies that examined grazing influences on the composition of desert-steppe grasslands in Mongolia. Similarly, few published accounts explore the relationship of environmental factors other than precipitation to plant community composition in Mongolia (Breymer and Klimek 1983). The aim of this study was to describe vegetation along apparent grazing gradients in three different ecological zones in Mongolia: the desert-steppe, steppe and mountain-steppe. Our specific research objectives were 1) to classify and describe plant communities sampled along grazing gradients in each of the three zones, and 2) to assess the relationship between the classified communities and measured environmental variables, including inferred relative grazing pressure.

Methods

Study areas

Study areas were located in three ecological zones along a precipitation gradient from the desert-steppe (42°25'N, 100°30'E), through the steppe (46°12'N, 100°10'E) to the mountain-steppe (46°27'N, 100°30'E), in Bayankhongor Aimag (province), Mongolia (Figure 1). All three ecological zones are dominated by perennial bunchgrasses and have been grazed by domestic livestock for at least 700 years and possibly several millenia. Mongolia has a continental climate, with cold, dry winters and warm, wet summers. Precipitation is unimodally distributed in all three zones with peak rainfall occurring in July. Mean annual temperature and precipitation are -1.7°C and 230 mm in the mountain-steppe, 1.6°C and 200 mm in the steppe and 4.8°C and 95 mm in the desert-steppe.

Sampling design

Plots were located along grazing gradients from water sources to areas distant from water. Livestock den-

sity and grazing pressure are usually highest close to water and decrease with distance away from water (Valentine 1947). Many investigators have sampled vegetation and soils along gradients from water sources to determine the effects of grazing on rangeland structure and function (Andrew and Lange 1986; Barker et al. 1989; Beeskow et al. 1995; Friedel 1997; Fusco et al. 1995; Thrash 1998; Tolsma et al. 1987; Tueller and Platou 1991; Turner 1998). In areas where it is logistically impossible to manipulate livestock densities experimentally, historical grazing gradients provide a way to observe the impacts of different grazing pressures on soils and vegetation. The principal drawback of this approach is that other environmental factors, such as slope, elevation, soil type or soil moisture content, may also vary with distance from water points, making it difficult to distinguish grazing effects from environmental effects. In the area of Mongolia where this study was conducted, detailed soil and vegetation maps that would have allowed precise stratification were lacking. Therefore, we collected data on key environmental factors at each plot (slope, aspect, elevation, soil texture and moisture, the activity of burrowing rodents), to help separate changes due to historical grazing pressure from those attributable to unrelated environmental gradients. In some cases, there were unavoidable correlations between distance from water and environmental gradients such as elevation.

To determine plot locations, all functioning wells and natural water sources in each zone were mapped on a 1:100,000 topographic map. The area surrounding each water source was stratified into three concentric categories: <500 meters from water, 500–2000 meters from water, and >2000 meters from water. An equal number of replicate plots was selected randomly in each distance-from-water category in each zone. In the steppe and mountain-steppe, 15 plots were sampled: five replicates in each distance-from-water category. In the desert-steppe, 27 plots were sampled, nine in each distance-from-water category. Each plot was sampled twice, once in summer 1994 and once in summer 1995.

Permanent plots with a 200-m radius were established from a fixed center point in each plot. Foliar cover of vegetation was sampled using the line-point method (Goodall 1952) along five 50-m transects on each plot for a total of 500 points per plot. Nomenclature follows Grubov (1982). In the desert-steppe the grasses *Stipa gobica* and *S. glareosa* were lumped in the vegetation analysis because they were indistin-

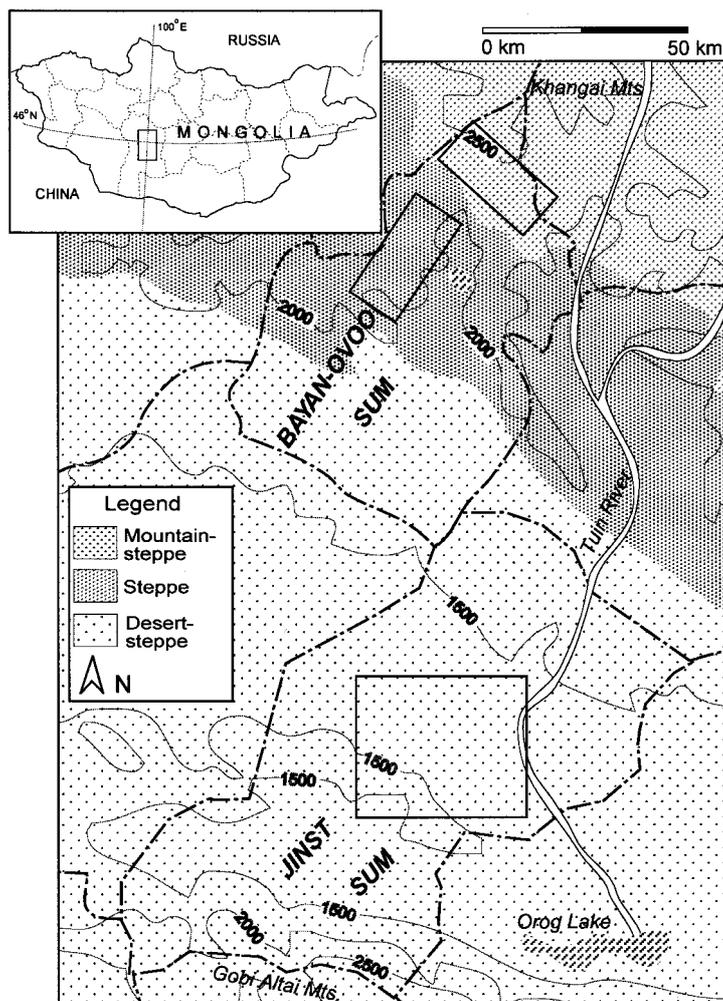


Figure 1. Map of study areas.

guishable in the field after seed set, when sampling was conducted. We obtained information on the life-history traits, palatability and response to disturbance of individual species from the previously cited literature on Mongolian vegetation, as well as the *Flora of the U.S.S.R.* and observations provided by local herders and Mongolian geobotanists.

Standing biomass, including both green and brown material, was clipped at 1.0 cm height in four systematically located circular 0.125 m² quadrats along each transect, for a total of 20 clipped samples per plot, then dried for 48 hours at 60 °C in the laboratory. Samples were separated into graminoid and forb fractions and weighed separately. Woody parts of subshrubs were included in the forb fraction. The biomass of large woody plants was not measured.

Soil samples were collected 2 m from the midpoint of three transects on each plot. In 1994, bulk density was sampled at 0–5 cm. After bulk density samples were dried and weighed in the lab, the samples from each plot were combined for analysis of soil organic C, total soil N, and available P and K. In 1995, samples were again taken from three transects on each plot at depths of 0–10 cm and 10–20 cm and analyzed for soil organic C, total soil N and percent coarse fraction.

Laboratory analyses of soil chemical composition were carried out at the Soil Science Department of the Institute of Geography and Geocryology of the Mongolian Academy of Sciences, Ulaanbaatar. Total soil N was determined using the Kjeldahl method (Bremner and Mulvaney 1982). Soil organic C was determined using Tyurin's method (Bel'chicova 1965).

Available P and K were determined using Machigin's methods (Machigin 1952; Kheifets 1965). All soil chemical analyses were conducted according to the Mongolian Standard Soil Testing Procedures (UST) (Baatar et al. 1994). The coarse fraction of soil is defined in this study as the fraction, by weight, greater than 1 mm in diameter, following Russian soil science protocols (Kachinskii 1958).

Statistical analyses

In all classification and ordination analyses each plot \times year combination was treated as a separate sample unit. This was done to increase the sample size for the classification and to determine if species composition remained constant or changed between years.

Two-way indicator species analysis (TWINSPAN) was used to classify the plots within each ecological zone into discrete plant communities (McCune and Mefford 1997). Plots in each ecological zone were analyzed separately. To reduce the influence of rare species on the classification, only species with absolute cover of 1% or greater in the steppe and cover of 2% or greater in the mountain-steppe were included in the analyses. Default cut levels (0, 2, 5, 10, 20) were used in the steppe and mountain-steppe. In the desert-steppe, where vegetation is extremely sparse, cut levels of 0, .5, 1, 3, 5 and 10 were used.

Tukey post hoc tests were used to determine which community groups in each zone differed significantly with respect to environmental variables and vegetation characteristics including total standing biomass, grass and forb biomass, total vegetation cover, and species richness and diversity.

Direct gradient analysis using CCA (canonical correspondence analysis) was used to detect environmental gradients in the vegetation data (McCune and Mefford 1997; Ter Braak 1987). Montecarlo tests (100 permutations) of constrained ordination scores against environmental variables were performed to assess the significance of the correlations.

Results

Mountain-steppe zone

Community classification and descriptions

A total of 83 species was documented (on $n = 15$ plots \times 2 years = 30 samples) of which 29 had cover values of at least 2% and were included in the classifi-

cation. Four community types were distinguished. *Festuca/Carex duriuscula/Artemisia adamsii* ($n = 5$) *Festuca/Koeleria macrantha/Artemisia laciniata* ($n = 4$) *Festuca/Koeleria macrantha/Potentilla bifurca* ($n = 8$) *Festuca/Koeleria macrantha/Poa attenuata* ($n = 13$)

Type 1) The *Festuca/Carex duriuscula/Artemisia adamsii* community occurred in heavily grazed and trampled streamside or streambottom areas (Table 1). Species composition was consistent with this history of heavy use by livestock. This community was dominated by *Festuca lenensis* and/or *F. valesiaca*, *Carex duriuscula*, *Agropyron cristatum*, *Koeleria macrantha* and *Artemisia frigida*. *Artemisia adamsii* was present on all but one plot in this group and was absent from plots in all other groups. *Koeleria* had lower cover values in this community than in all of the others. *C. duriuscula* and *A. adamsii* are both tolerant of grazing and known to increase with moderate to heavy grazing pressure (Pacyna 1986; Yunatov 1977). *A. adamsii* in particular is recognized as a disturbance indicator by range scientists and local herders (Fernandez-Gimenez 2000; Ulziikhutag 1985). While *C. duriuscula* is palatable to livestock, *A. adamsii* is unpalatable.

Average concentrations of P, K and N were highest; grass, forb and total biomass were lowest; and species diversity and richness were relatively high in this community compared with the other mountain-steppe communities identified by TWINSPAN (Table 2). We speculate that the relatively high concentrations of soil nutrients in these plots were the result of livestock redistributing nutrients in the landscape by voiding feces and urine near the water sources where they congregate.

Type 2) The *Festuca/Koeleria macrantha/Artemisia laciniata* community is dominated by *Festuca*, *K. macrantha* and *Agropyron cristatum* with co-dominants *Artemisia laciniata* and *Aster alpinus*. *A. laciniata* is unpalatable and *A. alpinus* only marginally palatable to livestock. *A. cristatum* is tolerant of grazing and a relative increaser under moderately heavy grazing pressure (Hilbig 1995). The plots in this type were also higher in mean elevation and had slightly steeper slopes than the other mountain-steppe communities.

Type 3) The *Festuca/Koeleria macrantha/Potentilla bifurca* community is dominated by typical mountain-steppe grasses (*Festuca* and *Koeleria*), with the addition of the rhizomatous grass *Elymus chinensis*, an increaser species (Hilbig 1995), *Agropyron*

Table 1. Summary of major plant species for 4 community types in the mountain-steppe ecological zone.

Species:	Percent cover and constancy by community type ^a							
	Type 1 n = 5		Type 2 n = 4		Type 3 n = 8		Type 4 n = 13	
	Cover	Constancy	Cover	Constancy	Cover	Constancy	Cover	Constancy
GRASSES & SEDGES:								
<i>Stipa krylovii</i>	0	0	0.8	25	3.9	88	5.3	92
<i>Festuca spp.</i>	12.6	100	22.7	100	18.4	100	21.2	100
<i>Koeleria macrantha</i>	9.2	100	14.3	100	13.7	100	16	100
<i>Agropyron cristatum</i>	5.9	100	5.2	100	5.4	100	4.9	85
<i>Poa attenuata</i>	2.2	60	3.5	75	1.4	38	4.4	77
<i>Elymus chinensis</i>	0.7	20	0.6	25	2.4	75	0	0
<i>Carex duriuscula</i>	16.0	100	2.0	50	3.5	75	0.6	23
<i>Carex korshinskyi</i>	0	0	0	0	0.4	13	0	0
<i>Carex spp.</i>	1.1	40	0.7	25	0	0	0	0
FORBS:								
<i>Thermopsis dahurica</i>	0	0	0	0	0	0	0.6	23
<i>Heteropappus hispidus</i>	0	0	0	0	1.4	50	1.7	38
<i>Pulsatilla spp.</i>	0	0	0.5	25	0	0	0.3	15
<i>Leontopodium leontopodoides</i>	0	0	0	0	0.3	13	0.5	8
<i>Artemisia monostachya</i>	0	0	0.6	25	0	0	0.2	8
<i>Taraxacum officinale</i>	0	0	0	0	0.3	13	0	0
<i>Thymus gobicus</i>	0	0	0	0	0.3	0	0	0
<i>Potentilla bifurca</i>	0	0	0	0	1.9	75	0	0
<i>Thalictrum foetidum</i>	0	0	1.7	50	0	0	0	0
<i>Astragalus depauperatus</i>	0	0	0.7	25	0	0	0	0
<i>Artemisia glauca</i>	1.0	40	0.7	25	5.6	88	2.7	62
<i>Potentilla strigosa</i>	0.8	40	0	0	0.6	25	0	0
<i>Aster alpinus</i>	0.4	20	3.6	100	0.4	13	0	0
<i>Artemisia laciniata</i>	0.6	20	3.8	100	0	0	0	0
<i>Arenaria capillaris</i>	2.0	60	1.3	50	0.6	25	1.0	31
<i>Artemisia adamsii</i>	5.4	80	0	0	0	0	0	0
<i>Artemisia frigida</i>	5.4	100	2.1	50	3.0	100	5.2	85
OTHER:								
Lichen cover	0	0	1.6	50	1.5	50	4.1	85
Moss cover	0.6	20	0	0	0	0	0	0

^aPercent cover is the mean percent cover for all plots in a community type. Constancy is the percent of plots in the type in which a species occurs.

cristatum, and the steppe bunchgrass *Stipa krylovii*. Forbs *Potentilla bifurca* and *Artemisia glauca* are co-dominant. The former is believed by some (Hilbig 1995) to increase with moderate grazing due to its prostrate growth form. The latter is a disturbance-associated species with little or no forage value for livestock (Ulziikhutag 1985). The presence of *A. glauca* may be associated with high levels of rodent (steppe mouse and marmot) activity on these plots. *A. glauca* may also increase in response to anthropogenic or livestock-induced disturbance, and is commonly found near animal bedding areas, nomadic encampments and other disturbed sites. This type had the

greatest forb biomass and the lowest total vegetative cover (82%) of the mountain-steppe communities.

Type 4) The *Festuca/Koeleria macrantha/Poa attenuata* community was dominated by mountain-steppe grasses (*Festuca*, *Koeleria* and *Poa*) together with *Agropyron cristatum* and *Stipa krylovii*. Important forbs in this community type included *Artemisia frigida*, *Artemisia glauca*, *Heteropappus hispidus* and *Thermopsis dahurica*. The plots in this community were located an average of 1185 meters from water. This community contained the lowest average number of species and species diversity of the four mountain-steppe communities, the highest total and grass

Table 2. Summary of selected environmental and vegetation characteristics of 4 community types in the mountain-steppe ecological zone (least squares mean \pm 1SE). (Means in the same row with same superscript are not significantly different at $P < 0.05$, Tukey post hoc test.)

	Type 1 n = 5	Type 2 n = 4	Type 3 n = 8	Type 4 n = 13
Distance from water (m)	40 \pm 10 ^a	225 \pm 103 ^a	175 \pm 64 ^a	1185 \pm 229 ^b
Elevation (m)	2316 \pm 16	2340 \pm 37	2328 \pm 29	2254 \pm 23
Slope (degrees)	6 \pm 1	10 \pm 1	8 \pm 1	6.8 \pm 0.6
Species richness	31.6 \pm 2.7 ^a	34 \pm 2.4 ^a	27.5 \pm 1.7 ^{ab}	23.5 \pm 1.4 ^b
Species diversity ^a	2.59 \pm 0.11 ^a	2.59 \pm 0.08 ^a	2.50 \pm 0.07 ^a	2.27 \pm 0.03 ^b
Total biomass (g/m ²)	47.1 \pm 2.0 ^a	53.6 \pm 3.0 ^{ab}	51.1 \pm 2.5 ^{ab}	63.0 \pm 5.0 ^b
Grass biomass (g/m ²)	31.5 \pm 1.6	37.4 \pm 3.3	34.7 \pm 3.0	47.3 \pm 3.8
Forb biomass (g/m ²)	15.5 \pm 1.2	16.2 \pm 1.78	16.36 \pm 1.1	15.7 \pm 1.8
Total cover %	83 \pm 2	86 \pm 3	82 \pm 3	88 \pm 1
Organic C % ^b	2.29 \pm 0.38	2.62 \pm 0.53	2.22 \pm 0.32	1.98 \pm 0.12
N % ^b	0.36 \pm 0.04	0.36 \pm 0.02	0.33 \pm 0.02	0.33 \pm 0.01
Available K (mg/100g)	22.52 \pm 0.48 ^a	19.08 \pm 1.07 ^{ab}	20.36 \pm 1.95 ^a	12.72 \pm 1.89 ^b
Available P (mg/100g)	1.27 \pm 0.07	1.11 \pm 0.03	1.17 \pm 0.06	1.16 \pm 0.10
% coarse fragments to 10 cm ^c	11.8 \pm 1.6 ^{ab}	9.8 \pm 2.7 ^{ab}	15.6 \pm 3.2 ^a	6.8 \pm 1.4 ^b
% coarse fragments 10 – 20 cm	15.1 \pm 1.4	10.0 \pm 0.4	17.5 \pm 5.4	10.9 \pm 2.5

^aDiversity was calculated using the Shannon-Wiener Diversity Index = $-\sum p_i \ln p_i$, where p_i = the proportion of cover of the i th species

^bSample sizes vary slightly for Type 3 and/or Type 2 for these variables

^cn = 4 for Type 3

biomass and the greatest total vegetative cover (88%). Nutrient concentrations were lowest (except for P), as were the percentages of coarse fragments in the soil at 0–10 cm and 10–20 cm, compared to the other mountain-steppe communities. The mean elevation of these plots was also slightly lower than the other communities.

Ordination

Direct gradient analysis with CCA produced eigenvalues of .227, .158 and .101 for the first three axes respectively (Figure 2). The eigenvalue represents the variance in the community matrix that is attributed to a particular axis (Jongman et al. 1995). Cumulatively, the three axes explain 39.3% of the variance in the community matrix. Monte Carlo tests determined the significance of the eigenvalues for all 3 axes to be $P < 0.05$.

Intraset correlations are the correlations of environmental variables and the “LC” scores obtained by regressing site scores from weighted averaging of the species scores on environmental variables (McCune and Mefford 1997). Intraset correlations may be useful indicators of the relative importance of environmental variables in structuring the ordination but do not indicate absolute importance. Since LC scores were used as the final scores in this ordination and to prepare the accompanying graphs, we report intraset

correlations as Palmer (1993) suggests. In the mountain-steppe, intraset correlations indicate that the first CCA axis is correlated with distance from water (.638) and negatively correlated with K (–.743) (Figure 2). The second axis is most strongly correlated with elevation (.647) and slope (.575). However, the null hypothesis that there was no relationship between the species matrix and environmental matrix was not rejected for the first axis in Monte Carlo tests ($P = 0.11$). Species-environment relationships were found to be significant for the second ($P = 0.02$) and third ($P = 0.01$) axes respectively.

Steppe zone

Community classification and descriptions

A total of 77 species was documented (on 30 plots) of which 40 had cover values of $\geq 1\%$ on at least one plot and were thus included in the classification. The resulting classification distinguished among four community types. *Achnatherum splendens/Chenopodium album* (n = 2) *Carex duriuscula/Artemisia adamsii* (n = 9) *Stipa krylovii/Cleistogenes squarrosa* (n = 15) *Poa attenuata/Artemisia frigida* (n = 4)

Type 5) The *Achnatherum splendens/Chenopodium album* type consisted of the same (outlier) plot sampled in two years. Though we do not consider this plot a good community type due to the lack of replication, the site is ecologically significant and

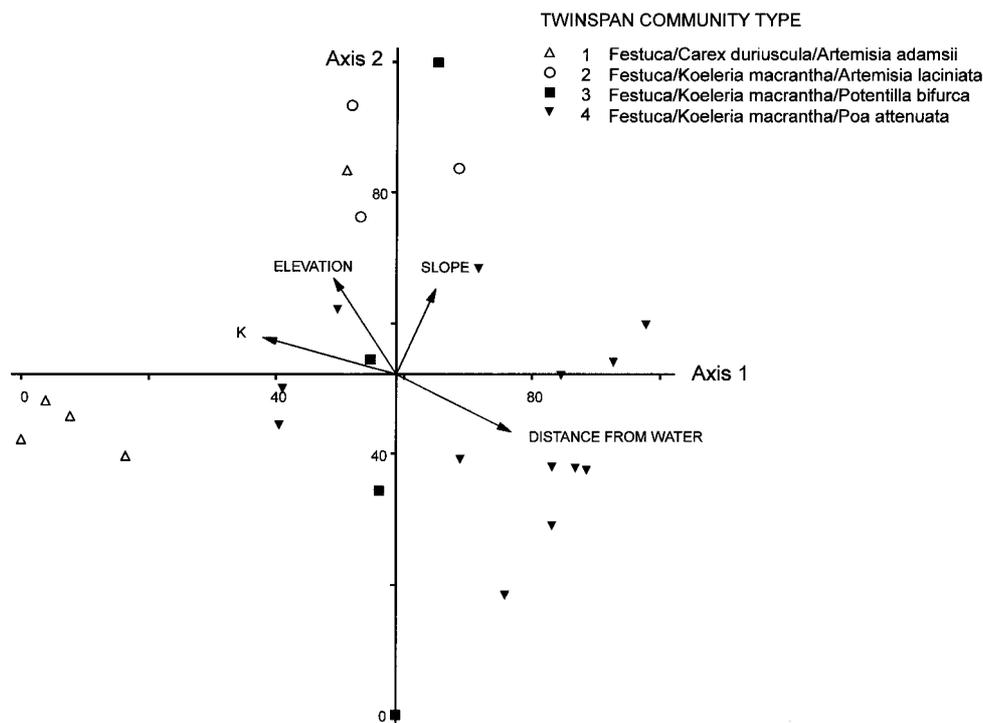


Figure 2. CCA biplot of sample sites and community types in the mountain-steppe zone, showing environmental variables.

therefore we describe it here (Table 3). The plot was located immediately adjacent to a heavily-used well and experienced high levels of disturbance by livestock. The prevalence of disturbance-associated species such as *Chenopodium album*, *C. acuminatum*, and *Lepidium densiflorum* is consistent with this history of use. *Achnatherum splendens*, which is associated with fluctuating groundwater and is most common in sandy soils around desert-steppe riparian areas, also is relatively unpalatable to livestock most of the year and thus may increase in relative cover on heavily grazed sites. This plot was distinguished by the absence of any of the typical steppe grasses (*Agropyron* or *Stipa*), and the profusion of ruderal forbs, particularly *Chenopodiums*. It had the lowest species richness and diversity of any of the community types in the steppe zone (Table 4). Total, forb and grass biomass were high, however, due to the dense cover of ruderal forbs and the mass of large *Achnatherum* plants. This plot was also an outlier with respect to the concentrations of P and K found in soils (more than three times the means for type 6, which had the next highest mean concentrations in the steppe zone). It also had the highest concentrations of N and C of the four steppe groups identified by TWINSpan. As with Type 1, the *Festuca lenensis*/

Carex duriuscula/*Artemisia adamsii* community of the mountain-steppe zone, we strongly suspect that the high levels of soil nutrients at this location were due to the deposition of fecal matter and urine by livestock when they came to the well to drink.

Type 6) The *Carex duriuscula*/*Artemisia adamsii* community was dominated by *Agropyron cristatum*, *Artemisia adamsii* and *Carex duriuscula*. *Stipa krylovii* was present on all but one of the plots in this type, and *Allium bidentatum* was present on all but two of the nine plots, in very high amounts on four of the plots. The dominant species are known to be grazing tolerant (*Agropyron cristatum*) or to increase in response to grazing (*Artemisia adamsii*, *Carex duriuscula*). *Elymus chinensis*, which was present on two of the plots, is a grazing-tolerant rhizomatous grass. This community also had significantly higher levels of soil P and K than community Types 7 or 8. Richness was significantly lower than in community Types 7 and 8. The *Carex duriuscula*/*Artemisia adamsii* community included six plots located <500 m from water, two plots 500–1000 m from water and one plot >2000 m from water. We suggest that the *Carex duriuscula*/*Artemisia adamsii* community is a grazing-induced community. It is similar to Type 1 in the mountain-steppe, except for the presence of *Stipa*

Table 3. Summary of major plant species for 4 community types in the steppe ecological zone.

Species:	Percent cover and constancy by community type							
	Type 5 n=2		Type 6 n=9		Type 7 n=15		Type 8 n=4	
	Cover	Constancy	Cover	Constancy	Cover	Constancy	Cover	Constancy
GRASSES & SEDGES:								
<i>Stipa krylovii</i>	0	0	4.2	89	5.7	100	7.1	100
<i>Stipa klemenzii</i>	0	0	1.6	44	2.2	47	0	0
<i>Agropyron cristatum</i>	0	0	8.2	100	10.6	87	7.7	75
<i>Koeleria macrantha</i>	0	0	0	0	4.5	93	11.6	100
<i>Cleistogenes squarrosa</i>	0	0	0	0	6.7	67	0.5	25
<i>Elymus chinensis</i>	0.5	50	1.5	22	0.1	7	0	0
<i>Poa attenuata</i>	0	0	0	0	0.1	7	2.7	100
<i>Achnatherum splendens</i>	15.5	100	0.3	22	0	0	0	0
<i>Carex duriuscula</i>	2.0	100	4.4	89	3.2	73	0.5	25
<i>Carex enervis</i>	0	0	0	0	0.1	7	0	0
<i>Carex spp.</i>	0	0	0.2	11	0	0	0.6	50
FORBS:								
<i>Arenaria capillaris</i>	0	0	0	0	0	0	0.3	25
<i>Astragalus laguroides</i>	0	0	0	0	0	0	0.3	25
<i>Artemisia frigida</i>	0	0	0	0	0.2	13	2.6	100
<i>Scorzonera divaricata</i>	0	0	0	0	0.1	7	1.6	100
<i>Thymus gobicus</i>	0	0	0	0	0.6	27	1.2	75
<i>Sibbaldienthe adpressa.</i>	0	0	0	0	0.2	7	0.4	25
<i>Allium anisopodium</i>	0	0	0	0	0.1	7	0.5	25
<i>Chamaerhodos erecta</i>	0	0	0	0	0.1	7	0	0
<i>Potentilla bifurca</i>	0	0	0	0	0.1	7	0	0
<i>Thermopsis dahurica</i>	0	0	0	0	0.1	7	0	0
<i>Astragalus galactites</i>	0	0	0	0	0.1	7	0	0
<i>Convolvulus ammanii</i>	0	0	0	0	0.4	20	0	0
<i>Cymbaria dahurica</i>	0	0	0	0	0.5	20	0	0
<i>Salsola pestifera</i>	0	0	0	0	0.1	7	0	0
<i>Dontostemon integrifolius</i>	0	0	0.2	11	1.1	40	0.5	25
<i>Ptilotrichum canescens</i>	0	0	0.2	11	0.8	27	1.2	75
<i>Heteropappus hispidus</i>	0	0	0.1	11	0.8	33	0	0
<i>Astragalus miniatus</i>	0	0	0.5	11	0.3	7	0	0
<i>Artemisia glauca</i>	0	0	0.1	11	0	0	0	0
<i>Allium bidentatum</i>	3.8	100	9.6	78	0	0	0	0
<i>Lepidium densiflorum</i>	7.4	50	4.3	56	0.1	13	0	0
<i>Artemisia adamsii</i>	7.8	100	17.2	100	11.0	93	3.2	50
<i>Chenopodium album</i>	6.5	100	0.3	22	0	0	0	0
<i>Chenopodium acuminatum</i>	16	100	0	0	0	0	0	0
SHRUBS:								
<i>Caragana pygmaea</i>	0	0	0	0	0.5	33	1.8	75

krylovii, a grass more commonly found in the steppe zone, and absence of *Festuca* species characteristic of the mountain-steppe.

Type 7) The *Stipa krylovii*/*Cleistogenes squarrosa* community was dominated by steppe bunch grasses and supported a diverse forb component including

Dontostemon integrifolius, *Cymbaria dahurica*, *Caragana pygmaea*, *Heteropappus hispidus*, *Ptilotrichum canescens* and *Thymus gobicus*. While disturbance-indicator species *C. duriuscula* and *A. adamsii* were present on most plots in this type, they accounted for relatively less cover than on plots in community Type

Table 4. Summary of selected environmental and vegetation variables for 4 community types in the Steppe ecological zone (least square means \pm SE). (Means in the same row with same superscript are not significantly different at $P < 0.05$, Tukey post hoc test.)

	Type 5 n = 2	Type 6 n = 9	Type 7 n = 15	Type 8 n = 4
Distance from water (m)	100	756 \pm 320	1660 \pm 260	2050 \pm 433
Elevation (m)	1960 ^a	2017 \pm 21 ^a	2027 \pm 14 ^{ab}	2105 \pm 3 ^b
Slope (degrees)	0 ^a	3 \pm 1 ^a	3 \pm 1 ^a	12 \pm 2 ^b
Species Richness	9 \pm 1 ^a	14.6 \pm 0.9 ^a	19.2 \pm 1.2 ^b	20.8 \pm 1.3 ^b
Species Diversity ^a	1.55 \pm 0.14 ^a	1.87 \pm 0.15 ^{ab}	2.10 \pm 0.07 ^{ab}	2.3 \pm 0.04 ^b
Total Biomass (g/m ²)	65.6 \pm 28.72 ^a	33.13 \pm 4.14 ^b	34.73 \pm 2.99 ^b	21.14 \pm 1.66 ^b
Grass Biomass (g/m ²)	23.36 \pm 0.24	13.11 \pm 2.09	18.90 \pm 2.34	12.76 \pm 0.59
Forb Biomass (g/m ²)	34.28 \pm 21.00 ^a	21.87 \pm 4.86 ^{ab}	15.78 \pm 1.79 ^{ab}	7.92 \pm 1.23 ^b
Total Cover %	67 \pm 16	59 \pm 4	65 \pm 3	58 \pm 5
Organic C % ^b	2.31 \pm 0.65	1.70 \pm 0.13	1.84 \pm 0.11	1.43 \pm 0.26
N % ^b	0.38 \pm 0.06	0.31 \pm 0.02	0.31 \pm 0.01	0.29 \pm 0.02
Available K (mg/100g)	127.00 ^a	37.27 \pm 5.15 ^b	22.03 \pm 1.52 ^c	20.45 \pm 0.32 ^c
Available P (mg/100g)	8.50 ^a	2.13 \pm 0.27 ^b	1.24 \pm 0.13 ^c	0.95 \pm 0.09 ^c
% coarse fragments to 10 cm	12.8	31.2 \pm 4.69	18.5 \pm 3.2	33.4 \pm 1.8
% coarse fragments 10–20 cm ^a	12.0 ^a	23.7 \pm 2.8 ^{ab}	21.4 \pm 2.5 ^a	35.1 \pm 0.08 ^b

^aDiversity was calculated using the Shannon-Wiener Diversity Index = $-\sum p_i \ln p_i$ in p_i = the proportion of cover of the i th species. ^bSample sizes vary slightly for Type 6 and/or Type 7 for these variables.

6. About half of the plots in this group were over 2000 meters from a water source and six were 500–2000 meters from water. Two plots in the group were within 500 meters of water. Both this community and the previous type (6) have similarities in species composition with Wallis de Vries et al. (1996) *Artemisia adamsii-Stipa krylovii*-lowland steppe with the exception that the communities described here lack *Artemisia frigida* and *Poa attenuata*, which are found at higher elevations.

Type 8) The *Poa attenuata/Artemisia frigida* community was dominated by steppe and mountain-steppe bunchgrasses and the subshrub *Artemisia frigida*, a species characteristic of the mountain-steppe. The plots in this type were located at a somewhat higher elevation than the other steppe plots, in the hills to the west of the broad valley containing most of the steppe plots. This slight variation in mean elevation between the Type 8 plots and the other steppe plots (approximately 100 meters), marks a difference between true steppe communities and a transition to the mountain-steppe zone. We suggest that the *Poa attenuata/Artemisia frigida* community represents a transition or ecotone community between the steppe and mountain-steppe ecological zones, and represents an environmentally-derived community. Concentrations of all nutrients were lowest in this community compared with the other steppe communities, as were biomass and cover, while diversity and richness were highest.

Ordination

Direct gradient analysis using CCA produced eigenvalues of .674, .322 and .261 respectively for axes 1, 2 and 3. The three axes cumulatively explained 40.3% of the variance in the community matrix. Monte Carlo tests indicate that all eigenvalues are significant at $P < 0.05$. Intrasets correlations indicate that the first axis is correlated with P (.941) and K (.928), and negatively correlated with distance from water (–.580) and elevation (–.443) (Figure 3a). The second axis is weakly correlated with distance from water (–.385) and elevation (–.312). Species-environment correlations on the first axis are significant at $P = 0.01$ and on the second axis at $P = 0.10$.

A second CCA analysis was performed without the outlier plot (Type 5 *Achnatherum splendens/Chenopodium album*), to determine if the same environmental variables drive the ordination in its absence (Figure 3b). Eigenvalues for this analysis were .460, .263 and .204 for the first three axes respectively, with a total of 41.2% of the variance in the community matrix explained cumulatively. Again in this analysis the first axis was correlated with P (.519) and K (.450), and negatively correlated with distance from water (–.633) and elevation (–.405). The second axis was correlated with percent coarse fraction at 10 cm (.671), at 20 cm (.478) and elevation (.525). Species-environment correlations on all axes were significant at $P < 0.05$. We concluded that in the absence of the

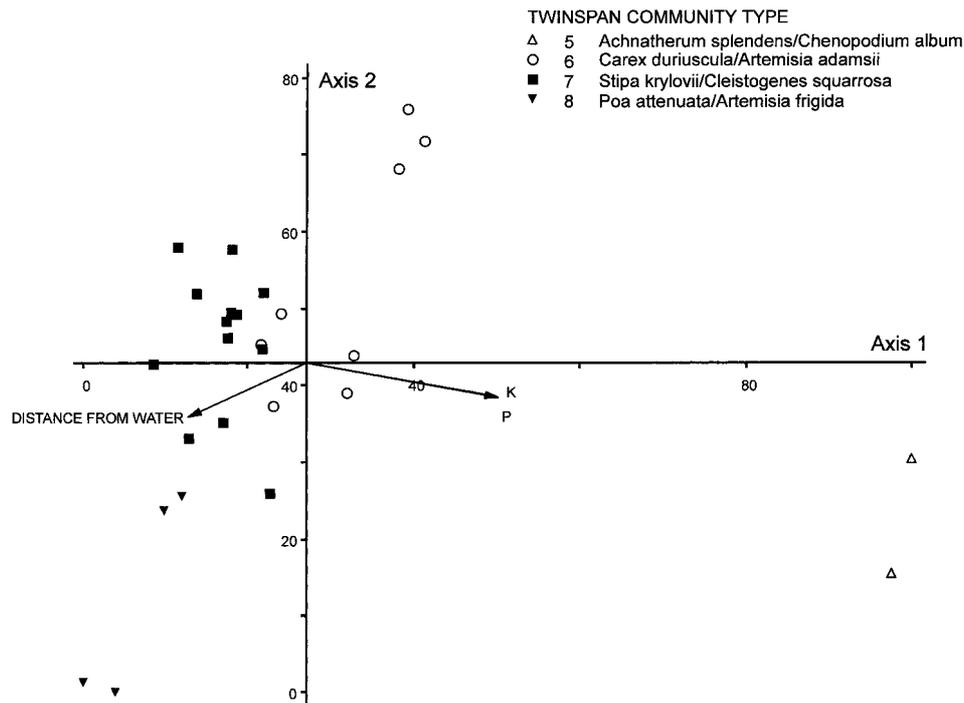


Figure 3a. CCA biplot of sample sites and community types in the steppe zone, showing environmental variables.

outlier plot, concentrations of P and K and distance from water remain the primary determinants of species composition in the steppe plots.

Desert-steppe zone

Community classification and descriptions

A total of 73 species was identified on 54 plots. Five communities were distinguished. *Reumuria songorica*/*Salsola passerina* (n = 2) *Stipa gobica*/*glareosa*/*Anabasis brevifolia* (n = 7) *Stipa gobica*/*glareosa*/*Cleistogenes songorica* (n = 31) *Stipa gobica*/*glareosa*/*Iris bungei*/*Caragana bungei* (n = 10) *Stipa gobica*/*glareosa*/*Artemisia schischkinii* (n = 4)

Type 9) The *Reumuria songorica*/*Salsola passerina* Type consisted of one plot sampled in two years and represents an extreme variant of the salt-shrub community (Type 10). As with Type 5 in the steppe (*Achnatherum splendens*/*Chenopodium spp.*), we do not consider this site a good community type, but include a description because of its ecological significance as example of a degraded salt shrub site (Table 5). This plot was located adjacent to a former brigade center (small settlement) and thus experienced high levels of livestock grazing and trampling

in addition to other anthropogenic activity, including vehicle traffic. Few steppe grasses were present on the site, which was dominated by salt shrub species *Reumuria songorica*, *Salsola passerina* and *Anabasis brevifolia*. Overall vegetation cover was sparse (9%), and most biomass was accounted for by salt shrubs. Species diversity and richness were very low (a total of six species was encountered on this plot over two years). Concentrations of C, P and K were higher than were observed in any of the other desert-steppe communities. This plot conforms with the description of the *Reumuria songorica* subassociation of the *Stipa glareosae*-*Anabasetum brevifoliae* identified by Hilbig (1995).

Type 10) *Stipa gobica*/*glareosa*/*Anabasis brevifolia* is a salt shrub community found on hard, stony sites. The dominant species include the desert-steppe grasses, *Stipa glareosa*/*gobica* and *Cleistogenes songorica*, and salt shrubs *Anabasis brevifolia* and *Salsola passerina*. Forbs *Allium polyrrhizum*, *Artemisia xerophytica* and *Ptilotrichum canescens* are also common. Mean vegetation cover for this type is 23%. This community strongly resembles the *Stipa glareosae*-*Anabasetum brevifoliae* community identified by Hilbig (1995). It not possible to determine whether this community is entirely edaphically derived, or

Table 5. Summary of major plant species for 5 community types in the desert-steppe ecological zone.

	Percent cover and constancy by community Type									
	Type 9 n=2		Type 10 n=7		Type 11 n=31		Type 12 n=10		Type 13 n=4	
	Cover	Constancy	Cover	Constancy	Cover	Constancy	Cover	Constancy	Cover	Constancy
GRASSES & SEDGES:										
<i>Stipa gobica\glareosa</i>	0.1	50	9.2	100	13.3	100	12.6	100	8.7	100
<i>Cleistogenes songorica</i>	0	0	0.2	57	1.1	97	0.5	60	0	0
<i>Achnatherum splendens</i>	0	0	0	0	0.1	10	0.2	10	0	0
<i>Elymus chinensis</i>	0	0	0	0	0.01	3	0.3	10	0.4	25
<i>Elymus racemosus</i>	0	0	0	0	0	0	0.5	20	0	0
<i>Eragrostis minor</i>	0	0	0	0	0.01	3	0	0	0	0
<i>Enneapogon borealis</i>	0	0	0.03	14	0	0	0	0	0	0
<i>Carex enervis</i>	0	0	0	0	0.2	23	0.1	30	0.05	25
<i>Carex spp.</i>	0	0	0	0	0.03	10	0.01	20	0	0
FORBS:										
<i>Haplophyllum dauricum</i>	0	0	0	0	0	0	0.04	20	0.7	50
<i>Corispermum sp.</i>	0	0	0	0	0.01	3	0.2	30	0.4	25
<i>Iris tenuifolia</i>	0	0	0	0	0.01	3	0.3	70	1.5	100
<i>Gypsophila desertorum</i>	0	0	0	0	0.1	10	0.02	20	0	0
<i>Convolvulus ammannii</i>	0	0	0	0	0.1	10	0.6	60	0	0
<i>Iris bungei</i>	0	0	0	0	0.4	55	1.5	100	0	0
<i>Scorzonera pseudodivariata</i>	0	0	0.1	29	0.2	23	0.7	90	0.4	75
<i>Allium mongolicum</i>	0	0	0.1	43	0.3	61	0.4	50	0.2	50
<i>Oxytropis aciphylla</i>	0	0	0.3	57	0.3	48	0.4	80	0.2	50
<i>Ajania achilleoides</i>	0	0	1.2	86	0.4	45	0.1	20	0.2	75
<i>Artemisia xerophytica</i>	0	0	0.3	71	1.9	94	0.04	10	0.7	75
<i>Allium polyrrhizum</i>	0	0	2.1	86	0.4	29	29	0.2	40	0
<i>Asparagus gobicus</i>	0	0	0.03	14	0.1	36	0.1	40	0	0
<i>Ptilotrichum canescens</i>	0	0	0.3	57	0.2	55	0.02	10	0	0
<i>Ajania fruticulosa</i>	0	0	0.1	14	0.1	3	0	0	0	0
<i>Bassia dasyphylla</i>	0.2	50	0.1	14	0.04	7	0	0	0	0
<i>Reaumuria soongorica</i>	2.8	100	0.4	43	0.1	16	0	0	0	0
<i>Salicornia europaea</i>	0.1	50	0.4	14	0	0	0	0	0	0
<i>Salsola passerina</i>	5.6	100	0.5	100	0.1	13	0	0	0	0
<i>Anabasis brevifolia</i>	0.1	50	1.2	100	0.1	29	0	0	0	0
SHRUBS:										
<i>Atraphaxis pungens</i>	0	0	0	0	0	0	1.0	50	0	0
<i>Caragana bungei</i>	0	0	0	0	0.1	10	2.2	90	0.5	25
<i>Zygophyllum xanthoxylon</i>	0	0	0	0	0.01	3	0.2	10	0	0
<i>Artemisia schischkinii</i>	0	0	0.9	29	0.01	3	0	0	3.0	100
<i>Caragana leucophloea</i>	0	0	0	0	0.2	36	0.8	90	1.5	100
<i>Eurotia ceratoides</i>	0	0	0.3	43	0.1	19	0.2	19	0	0
<i>Convolvulus gortschakovii</i>	0	0	0	0	0.1	7	0.1	20	0	0

whether long-term anthropogenic impacts that lead to soil compaction and surface soil loss, might also influence species composition.

Type 11) *Stipa gobica\glareosa/Cleistogenes songorica* is a desert-steppe grassland community dominated by *Stipa* species common to the desert-steppe

and *Cleistogenes songorica*, a small-statured bunch grass, with subshrub *Artemisia xerophytica* co-dominant. Other common forbs include *Ajania achilleoides*, *Ptilotrichum canescens*, *Allium mongolicum* and *Oxytripis aciphylla*. Plots transitioning to salt shrub communities may contain *Anabasis brevifolia*,

Table 6. Summary of selected environmental and vegetation variables for the desert-steppe (least squares mean \pm 1 SE). (Means in the same row with same superscript are not significantly different at $P < 0.05$, Tukey post hoc test.)

	Type 9 n=2	Type 10 n=7	Type 11 n=31	Type 12 n=10	Type 13 n=4
Distance from water (m)	400	2500 \pm 896	1710 \pm 247	1820 \pm 266	3300 \pm 693
Elevation (m)	1360	1380 \pm 3	1374 \pm 2	1378 \pm 2	1380 \pm 0
Slope (degrees)	0	2 \pm 1.5	2 \pm 0.5	0	1 \pm 0.6
Species richness	4 \pm 2 ^a	11 \pm 1.3 ^{bc}	10 \pm 0.6 ^b	13.4 \pm 0.6 ^c	10.5 \pm 1.3 ^{abc}
Species diversity ^a	0.83 \pm 0.21 ^a	1.57 \pm 0.16 ^b	1.17 \pm 0.05 ^a	1.58 \pm 0.09 ^b	1.63 \pm 0.07 ^b
Total biomass (g/m ²) ^b	16.5 \pm 9.24	10.75 \pm 2.34	9.57 \pm 0.98	10.37 \pm 1.02	13.60 \pm 5.6
Grass biomass (g/m ²) ^b	0 \pm 0 ^a	4.09 \pm 0.90 ^{ab}	6.10 \pm 0.55 ^b	7.76 \pm 0.98 ^b	4.3 \pm 1.5 ^{ab}
Forb biomass (g/m ²)	1.85 \pm 0.94 ^a	0.82 \pm 0.22 ^{ab}	0.43 \pm 0.08 ^b	0.33 \pm 0.07 ^b	1.02 \pm 0.52 ^{ab}
Total cover %	9 \pm 2 ^a	23 \pm 3.2 ^b	26 \pm 1.1 ^b	27 \pm 1.5 ^b	21 \pm 3.4 ^{ab}
Organic C % ^b	1.49 \pm 0.93	1.00 \pm 0.21	1.03 \pm 0.11	1.01 \pm 0.21	0.68 \pm 0.02
N % ^b	0.24 \pm 0.12	0.21 \pm 0.03	0.43 \pm 0.08	0.33 \pm 0.07	1.02 \pm 0.52
Available K (mg/100g) ^b	22.80	12.60 \pm 2.89	15.03 \pm 1.33	13.15 \pm 1.56	10.30 \pm 1.56
Available P (mg/100g) ^b	1.80 ^a	0.99 \pm 0.11 ^b	0.95 \pm 0.07 ^b	0.75 \pm 0.10 ^b	1.15 \pm 0.03 ^{ab}
% coarse fragments to 10 cm ^b	13.3 ^{ac}	30.5 \pm 5.1 ^b	20.8 \pm 0.8 ^a	18.9 \pm 1.56 ^{ac}	9.4 \pm 4.8 ^c
% coarse fragments 10 – 20 cm ^b	9.5 ^{ab}	26.4 \pm 6.6 ^{ab}	20.0 \pm 1.7 ^a	32.8 \pm 4.0 ^b	19.3 \pm 0.05 ^{ab}

^aDiversity was calculated using the Shannon-Wiener Diversity Index = $-\sum p_i \ln p_i$, where p_i = the proportion of cover of the i th species.

^bSample sizes for Group 11 and/or Group 12 vary slightly for these variables.

Reumuria soongorica and/or *Salsola passerina*. The community averages 26% vegetative cover. This group resembles the community identified by Hilbig as *Allio polyrrhizi-Stipetum glareosae* with the exception that *Allium polyrrhizum* is less frequent on these plots than the more common forbs mentioned above.

Type 12) *Stipa gobica*:*glareosa*/*Iris bungei*/*Caragana bungei* differs from the desert-steppe grassland described above in the constant presence of shrub species *Caragana bungei* and *C. leucophloea*. *Iris bungei* is co-dominant with the *Stipa* species and *C. bungei*. Other forbs common to this type include *Scorzonera pseudodivaricata*, *Convolvulus amannii* and *Oxytropis aciphylla*. The shrubs *Atraphaxis pungens* and *Eurotia ceratoides* are also frequent in this community. *Elymus racemosus* occurs at relatively high densities on the most sandy sites. This community usually occurs on sandy sites, averages 27% vegetative cover and has highest grass biomass, richness and diversity of all the desert-steppe communities identified by TWINSPAN.

Type 13) The *Stipa gobica*:*glareosa*/*Iris tenuifolia* community consisted of two plots (each sampled twice), which might be considered a sub-association of the desert shrub-steppe described above. It differs from Type 12, the *Stipa gobica*:*glareosa*/*Iris bungei*/*Caragana bungei* community, in the absence of *C. bungei* and *I. bungei*, the increased dominance of *I. tenuifolia* and *C. leucophloea*, and the presence of the shrub *Artemisia schischkinii*.

Ordination

Direct gradient analysis of all desert-steppe plots with CCA produced eigenvalues of .317, .245 and .170 for the first three axes. Cumulatively, these axes explain 21.3% of the variance in the community matrix. Monte Carlo tests found eigenvalues for all three axes to be significant ($P < 0.05$). Intrasect correlations indicate that the first axis is correlated with percent coarse fragments to 10 cm depth (.507) and negatively correlated with bulk density (–.650) (Figure 4). In this zone, higher bulk density is associated with sandy sites (rather than soil compaction) whereas sites with a high percentage of coarse fragments tend to have a pebble-covered soil surface. The second axis is correlated with P (.692). Monte Carlo tests indicate that significant species-environment correlations exist for the first axis ($P = 0.03$), but not for the second ($P = 0.33$) and third ($P = 0.17$).

Since we felt that the outlier plot (Type 9 *Reumuria soongorica*/*Salsola passerina*) might unduly influence the ordination, we also performed CCA on the remaining samples, removing the two samples representing that plot. This analysis produced (statistically significant at $P < 0.05$) eigenvalues of .329, .175 and .136 respectively, explaining a cumulative 22.0% of the variance in the community matrix. Intrasect correlations showed axis 1 correlated with coarse fraction to 10 cm (.514) and negatively correlated with bulk density (–.618), just as with the pre-

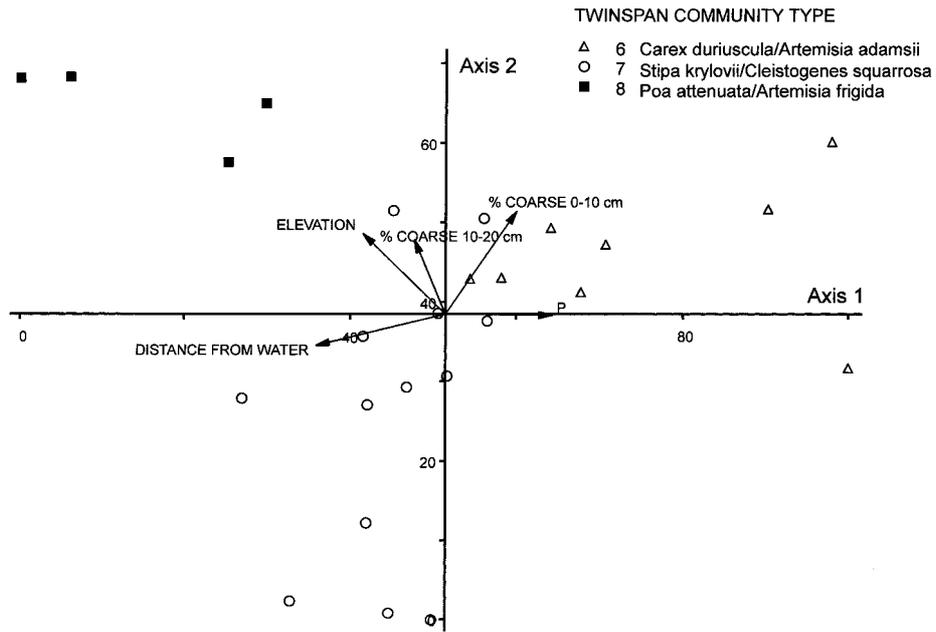


Figure 3b. CCA biplot of sample sites and community types in the steppe zone, omitting outlier plots in community Type 5.

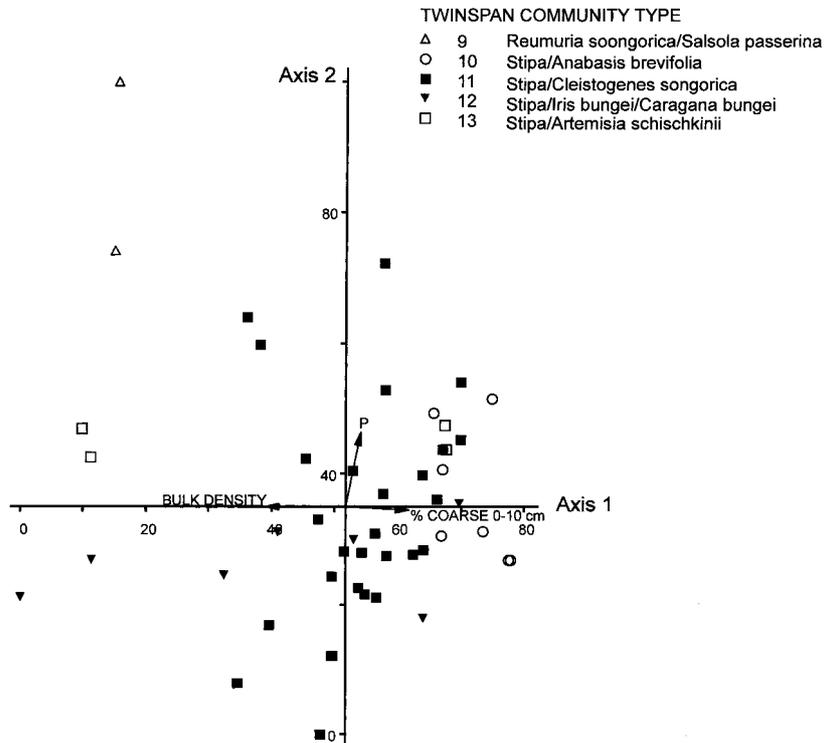


Figure 4. CCA biplot of sample sites and community types in the desert-steppe zone, showing environmental variables.

vious analysis. The second axis was correlated with distance from water (.675) and negatively correlated with K (-.410), potentially indicating a grazing influ-

ence on community composition. However, Monte Carlo tests indicated that species-environment correlations for the second axis were not significant.

Finally, in order to determine if the effects of a grazing gradient might be detectable when community differences likely driven by edaphic factors were removed from the analysis, we conducted a CCA analysis on samples ($n=31$) from Type 11 only (*Stipa gobica*'*glareosa*/*Cleistogenes songorica*). Eigenvalues for this analysis were .155, .145 and .135 with 28.9% of the variance in the community matrix cumulatively explained. All eigenvalues were significant in Monte Carlo tests ($P < 0.05$). Intraspecific correlations indicated that the first CCA axis is negatively correlated with coarse fraction at 20 cm (-.730) and correlated with distance from water (.468). The second axis is correlated with P (.540), elevation (.400) and negatively correlated with bulk density (-.411). Species-environment relationships for all three axes were significant ($P < 0.05$) according to Monte Carlo tests. TWINSpan analysis conducted on the 31 plots within community 11 divided the community into two main subassociations, one found on sandier sites distinguished by the presence of *Caragana* shrubs and associated forbs, including one annual present only in rainy-year (1994) samples (*Erodium tibetanum*), the other found on sites higher in P and characterized by the presence of salt-shrub species.

Discussion

Vegetation change along grazing gradients

In the steppe and mountain-steppe zones, vegetation changes along gradients from water sources were consistent with typical patterns of vegetation change in response to increasing grazing pressure, despite potentially confounding elevation influences. In both the mountain-steppe and the steppe, the vegetation factors driving the classification were the presence/absence of ruderal species and the presence/absence of highly palatable steppe grasses. These two functional groups typically respond in opposite fashions to increasing grazing pressure, with ruderal species increasing and palatable grasses decreasing. In both the mountain-steppe and steppe zones, the cover of ruderal species was highest in plots closest to water, where livestock activity is concentrated. Species of marginal palatability and grazing-tolerant species were also more abundant near water and at intermediate distances from water. Although the steppe grasses typical of each zone were present on most plots, they were less abundant on the heavily grazed

plots close to water, and some grasses were absent on the most heavily disturbed plots.

No consistent vegetation changes attributable to grazing gradients were observed in the desert-steppe. Vegetation factors driving the classification were the presence/absence of salt-shrub species and the presence/absence of *Caragana* shrubs, *Iris bungei* and *I. tenuifolia*, species with affinities for sandy sites. In this arid and variable zone, species composition appeared to be driven by edaphic factors. With the exception of one outlier plot, the dominant desert-steppe grass, *Stipa gobica*'*glareosa*, was present on every plot. Even when the samples from one community type (Type 11) were analyzed with TWINSpan in an attempt to control for community differences driven by edaphic factors, the same pattern emerged, and samples within this type were divided into two main groups based on the presence of *Caragana* species, or salt shrub species. Both *Caragana* species and most salt shrubs are valued forage for camels, but we found no information on their response to browsing, making it difficult to interpret these communities in relation to grazing gradients. We did observe that the *Caragana* communities tended to occur on sandier soils, and the salt shrub communities were most often found on harder, stony soils. We suggest two possible interpretations: either grazing has little influence on community composition in the desert-steppe, an outcome consistent with some theories of vegetation dynamics in semi-arid systems (Milchunas et al. 1988; Ellis and Swift 1988), or the effects of the grazing gradient were overwhelmed by patchiness in soil types along distance from water gradients. Additional research is needed to distinguish between grazing and edaphic influences on desert-steppe vegetation.

Unlike many rangelands in Africa (Moleele and Perkins 1998; Tolsma et al. 1987) and North America (Archer 1989; McPherson et al. 1988), heavy grazing does not appear to be associated with encroachment by shrubs in these Mongolian study areas. This may be because browsing pressure from goats and camels suppresses expansion. (Goats and camels account for a significant proportion of herd composition in dry steppe and desert-steppe areas.) It might also be attributable to the fact that herders in the desert-steppe use shrubs as fuelwood, and impacts of fuelwood harvesting would most likely be greatest close to wells and water sources where herders prefer to camp. However, Mongolian herders value many species of shrubs and try to avoid harvesting live plants, preferring to pull up dead shrubs by their roots. Another

possibility is that the shrub species observed at the study sites are unable to outcompete grasses for limited water or nutrients under the current conditions, even in areas of heavy grazing pressure.

Although rodent activity was not an important factor driving species composition according to CCA, our field observations suggest that the burrowing activities of the steppe vole (*Microtus brandti*) and marmot (*Marmota spp.*), probably affect species composition in the steppe and mountain-steppe zones, and may interact with livestock grazing to influence community structure. For example, the presence of *Artemisia glauca* in Types 3 (*Festuca/Koeleria macrantha/Potentilla bifurca*) and 4 (*Festuca/Koeleria macrantha/Poa attenuata*) in the mountain-steppe was often associated with marmot burrows. Similarly, the profusion of *A. adamsii* on plots close to water in the steppe and mountain-steppe was associated with steppe mouse burrows and trails as well as heavy grazing pressure. No statistically significant relationships between rodent activity and distance from water were detected. However, interaction between livestock impacts and the impacts of concurrent disturbance regimes, including rodents, in Mongolia deserves further attention, particularly since herders consistently identify rodents as one of the major causes of pasture degradation.

TWINSPAN classification indicated that species composition remained relatively stable over the two years during which species cover was assessed on each plot. In the mountain-steppe, 3 of 15 plots changed types between sampling years, while 1 of 15 plots in the steppe and 3 of 27 plots in the desert-steppe shifted between years. In the desert-steppe, the proportion of cover of salt-shrub community species increased in the drier year (1995) in the three plots that changed types. There were no consistent patterns of change in the mountain-steppe. Most plots were classified in the same community type for both years in all zones. Thus, even though the two sampling years differed dramatically in rainfall, with precipitation nearly twice the average in 1994 and precipitation from one to ten percent of the average in 1995, overall changes in composition were not sufficient to shift plots from one community type to another. This suggests that the classification reflects relatively stable assemblages of species that are not dramatically altered by interannual variations in precipitation, and which differ from each other due to variations in long-term grazing intensity in the steppe and mountain-steppe and edaphic characteristics in the desert-

steppe. In another study on the same plots (Fernandez-Gimenez and Allen-Diaz 1999), we found that the cover of 33% of desert-steppe species, 50% of steppe species, and 33% of mountain-steppe species differed significantly between years. Thus, although the cover of many individual species fluctuated between years in all three zones, the communities we identified varied little over the same (brief) time period.

These apparently stable communities could be interpreted as "grazing equilibria," communities selected for over millennia of grazing, and which would not be expected to change dramatically between years. On the other hand, in a mesic environment with a long evolutionary history of grazing, such as the mountain-steppe, we expect that a change in grazing regime would result in a shift in community composition, as the conventional range succession model (Dyksterhuis 1949) and Milchunas et al. (1988) predict. Accordingly, we interpret the grazing-induced community types we identified in the steppe and mountain-steppe as alternate vegetation states for their respective ecological zones, which differ in floristic composition largely due to historical grazing pressure. We do not know how the identified communities respond to the removal of grazing, and believe this question deserves further study in Mongolia. The work of Mongolian plant ecologists suggests that mountain-steppe pastures shift in composition with long-term grazing removal (Lhagvajav 1993 unpublished data & personal communication).

Community-environment relationships

The ordinations within each of the three zones were largely driven by soil factors, especially nutrient concentrations. In the steppe zone, P and K were highly correlated and both influenced the ordinations. In the mountain-steppe K played a more important role. In the desert-steppe soil physical characteristics as indicated by percent coarse to 10 cm depth and bulk density drove the ordination together with P. In all three zones, concentrations of P, K, N and C were usually greatest on the plots closest to water. Since distance from water and concentrations of P and K were negatively correlated, it is possible (and we believe likely) that livestock mediated the redistribution of nutrients along a gradient from water sources. Similar patterns of nutrient redistribution around water points have been observed by other investigators (Moleele and Perkins 1998; Tolsma et al. 1987; Turner 1998). Tolsma et al. (1987) and Turner (1998) both observed

higher concentrations of P near water points relative to outlying areas, as well as elevated concentrations of P in plant tissue collected near water points. Moleele and Perkins (1998) observed elevated N concentrations near water points.

Distance from water, which we assumed to be inversely correlated with relative grazing pressure, also played a significant role in the ordination of steppe and mountain-steppe communities. The gradient in livestock densities and relative grazing pressure with distance from water may have influenced plant community composition both directly, through defoliation and its associated effects, and indirectly, by increasing the relative concentrations of certain nutrients close to water. In the steppe and mountain-steppe, communities dominated by ruderal or grazing-tolerant species occurred close to water on sites with elevated nutrient concentrations. More work is needed to assess the effects of nutrient enrichment and depletion on the productivity and competitive success of important plant species in each zone. Tolsma et al. (1987) and Moleele and Perkins (1998) each suggest that particular species associated with intense grazing pressure and found near water points may also be favored by elevated N concentrations in these areas. In this study, high nutrient concentrations near water sources in the steppe zone may have affected both plant composition and productivity, as the high biomass and cover levels in Type 5, the *Achnatherum splendens/Chenopodium album* site, suggest. Hilbig (1995) reports the presence of *C. album* on disturbed and nutrient-enriched relevés in Mongolia, where it occurs with other nitrophilous species such as *Urtica cannabina*. A somewhat surprising result of our study is the greater differences in, and influence of, P and K along grazing gradients, compared with N, commonly the most limiting nutrient on rangelands, other than water.

Summary and conclusions

The vegetation factors driving classifications were the presence/absence of disturbance-associated (ruderal) species and highly palatable grasses in the steppe and mountain-steppe, and salt-shrub species and *Caragana* shrubs in the desert-steppe. Plots were relatively stable between years in all three zones, suggesting that our classifications are robust to interannual variations in species composition due to fluctuating precipitation. Several of the identified types corre-

spond with communities previously classified using phytosociological methods, lending further support to the robustness of these classifications. A limitation of our study was the potential correlation of our grazing gradients with other environmental factors. More controlled studies of the effects of different grazing intensities as well as grazing removal are needed to better understand livestock-mediated vegetation change in Mongolian steppe ecosystems.

The ordination of communities within each zone was largely driven by soil nutrient concentrations, particularly P and K, in all three zones. Soil physical characteristics also played an important role in the desert-steppe and steppe. Distance from water, which was negatively correlated with P and K, and assumed to be correlated with relative grazing pressure, was also a significant driving factor in classifications in the steppe and mountain-steppe zones (but not in the desert-steppe when all plots were considered). We speculate that elevated nutrient concentrations near water (and in communities with high proportions of ruderal and grazing-tolerant species) are the result of livestock redistributing nutrients in the landscape by voiding urine and feces in the areas where they congregate. We further suggest that grazing livestock may thus have affected plant community composition both directly and indirectly. Direct effects are visible in the increased proportion of ruderal and grazing-tolerant species, and decreased proportion of highly palatable grasses, in communities close to water. Livestock may affect plant community composition, biomass and cover indirectly by depositing nutrients in the vicinity of water sources, and possibly by removing nutrients from areas distant from water. This hypothesis deserves further testing under more controlled conditions.

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References

- Andrew M.H. and Lange R.T. 1986. Development of a new piosphere in arid chenopod shrubland grazed by sheep 2. Changes to the vegetation. *Australian Journal of Ecology* 11: 411–424.
- Archer S. 1989. Have southern Texas savannas been converted to woodlands in recent history?. *American Naturalist* 134: 545–561.
- Baatar R., Ochirbal C., Maasursen D., Dorjgotov S., Solongo G., Javzandolam D. et al. 1994. Soil Testing Methods, MPR National Standards (in Mongolian). Ulsiin Standartiin Khevlekh Uildver, Ulaanbaatar.
- Barker J.R., Herlocker D.J. and Young S.A. 1989. Vegetal dynamics along a grazing gradient within the coastal grassland of central Somalia. *African Journal of Ecology* 27: 283–289.
- Beeskov A.M., Elissanlede N.O. and Rostagno C.M. 1995. Ecosystem changes associated with grazing intensity on the Punta Ninfas rangelands of Patagonia, Argentina. *Journal of Range Management* 48: 517–522.
- Bel'chicova N.P. 1965. Determination of the humus of soils by I.V. Tyurin's method. In: *Agrochemical methods in study of soils*. 4th edn. Izdatel'stvo Nauka, Moscow, pp. 75–102.
- Bremner J.M. and Mulvaney C.S. 1982. Nitrogen—total. In: Page A.L. (ed.), *Methods of soil analysis*, part 2, chemical and microbial properties. American Society of Agronomy, Madison, WI, pp. 599–611.
- Bremeyer A. and Klimek K. 1983. Mongolian dry steppe geosystems, a case study of Gurvan Turuu area. Polish Academy of Sciences Institute of Geography and Spatial Organization, Geographical Studies Issue No 2.
- Chogni O. 1989. Methods for the protection and restoration of pasture. In: Tserendolam R. and Tserendash S. (eds), *Current state of natural pasture use and protection, proceedings of a scientific conference* (in Mongolian). J. Sambuugiin Neremjit Mal Aj Akhuin Erdem Shinjilgeenii Khureelegiin Belcheer Tejeeliin Salbar, Ulaanbaatar, pp. 12–14.
- Dyksterhuis E.J. 1949. Condition and management of rangeland based on quantitative ecology. *Journal of Range Management* 2: 104–115.
- Ellis J.E. and Swift D.M. 1988. Stability of African pastoral ecosystems: alternate paradigms and implications for development. *Journal of Range Management* 41: 450–459.
- Fernandez-Gimenez M.E. and Allen-Diaz B.H. 1999. Testing a non-equilibrium model of rangeland vegetation dynamics in Mongolia. *Journal of Applied Ecology* 36: 871–885.
- Fernandez-Gimenez M.E. 2000. The role of Mongolian nomadic pastoralists' ecological knowledge in rangeland management. *Ecological Applications* 10: 1318–1326.
- Friedel M.H. 1997. Discontinuous change in arid woodland and grassland vegetation along gradients of cattle grazing in central Australia. *Journal of Arid Environments* 37: 145–164.
- Fusco M., Holochek J., Tembo A., Daniel A. and Cardenas M. 1995. Grazing influence on watering point vegetation in the Chihuahuan desert. *Journal of Range Management* 48: 32–38.
- Goodall D.W. 1952. Some considerations in the use of point quadrats for the analysis of vegetation. *Australian Journal of Science Research Series B5*: 1–41.
- Grubov I.V. 1982. Key to Mongolian vascular plants with illustrations (in Russian). Nauk, Leningrad.
- Hilbig W. 1995. The vegetation of Mongolia. SPB Academic Publishing, Amsterdam.
- Jongman R.H.G., Ter Braak C.J.F. and Van Tongeren O.F.R. 1995. *Data analysis in community and landscape ecology*. Cambridge University Press, Cambridge.
- Kachinskii N.A. 1958. Mechanical and microaggregational composition of soil, methods of its study (in Russian). Izd-vo AN SSSR.
- Kheifets D.M. 1965. Methods for determination of phosphorus in soils. In: *Agrochemical methods in study of soils* (translated from Russian). 4th edn. Izdatel'stvo "Nauka", Moscow, pp. 143–225.
- Komarova V.L. 1968. Flora of the U.S.S.R. Israel Program for Scientific Translations (for NSF), Jerusalem.
- Lhagvajav N. 1992. Monthly and seasonal pasture growth in alpine zone pastures. In: *Results of scientific research and analysis* (in Mongolian). Shinjleekh Okhan Tekhnikii Medeeliin Tuv, Ulaanbaatar, pp. 50–54 Results of scientific research and analysis (in Mongolian). Shinjleekh Okhan Tekhnikii Medeeliin Tuv, Ulaanbaatar.
- Machigin B.P. 1952. *Methods of Agrochemical, Agrophysical and Microbiological Research in Irrigated Cotton Areas* (in Russian). Izd-voAN UzSSR, Tashkent.
- McCune B. and Mefford M.J. 1997. *Multivariate Analysis of Ecological Data*. MjM Software Design, Gleneden Beach, OR.
- McPherson G.R., Wright H.A. and Webster D.B. 1988. Patterns of shrub invasion in semiarid Texas rangelands. *American Midland Naturalist* 120: 391–397.
- Milchunas D.G., Sala O.E. and Lauenroth W.K. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *The American Naturalist* 132: 87–106.
- Moleele N.M. and Perkins J.S. 1998. Encroaching woody plant species and boreholes: is cattle density the main driving factor in the Olifants Drift communal grazing lands, south-eastern Botswana?. *Journal of Arid Environments* 40: 245–253.
- Pacyna A. 1986. *Fragmenta Floristica et Geobotanica*. XXX: 313–451.
- Palmer M.W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology* 74: 2215–2230.
- Ter Braak C.J.F. 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio* 69: 69–77.
- Thrash I. 1998. Impact of large herbivores at artificial watering points compared to that at natural watering points in Kruger National Park, South Africa. *Journal of Arid Environments* 38: 315–324.
- Tolsma D.J., Ernst W.H.O. and Verwey R.A. 1987. Nutrients in soil and vegetation around two artificial waterpoints in eastern Botswana. *Journal of Applied Ecology* 24: 991–1000.
- Tserendash S. and Erdenebaatar B. 1993. Performance and management of natural pasture in Mongolia. *Nomadic Peoples* 33: 9–15.

- Tsogoo D. 1990. Proper utilization methods for mountain forest steppe hay meadows of the MPR (in Mongolian). PhD Dissertation, Mongolian National University, Ulaanbaatar.
- Tueller P.T. and Platou K.A. 1991. A plant succession gradient in a big sagebrush/grass ecosystem. *Vegetatio* 94: 57–68.
- Turner M.D. 1998. Long-term effects of daily grazing orbits on nutrient availability in Sahelian West Africa: I. Gradients in the chemical composition of rangeland soils and vegetation. *Journal of Biogeography* 5: 669–682.
- Ulziikhutag N. 1985. Key to forage plants of the pasture and hayfields of the MPR (in Mongolian). Ulsiin Kheveleliin Gazar, Ulaanbaatar.
- Ulziikhutag N. 1989. Survey of Mongolian vegetation provinces (in Mongolian). Ulsiin Kheveleliin Gazar, Ulaanbaatar.
- Valentine K.A. 1947. Distance from water as a factor in grazing capacity of rangeland. *Journal of Forestry* 45: 749–754.
- Wallis de Vries M.F., Manibazar N. and Dugerlham S. 1996. The vegetation of the forest-steppe region of Hustain Nuruu, Mongolia. *Vegetatio* 122: 111–127.
- Yunatov A.A. 1977. Fundamental characteristics of the vegetation of the Mongolian People's Republic (in Mongolian). Ulsiin Kheveleliin Gazar, Ulaanbaatar.