Japanese Society of Grassland Science ISSN1744-6961

ORIGINAL ARTICLE

# Positive and negative effects of livestock grazing on plant diversity of Mongolian nomadic pasturelands along a slope with soil moisture gradient

Noboru Fujita[1], Narantsetsegiin Amartuvshin[2], Yasuhiro Yamada[1], Kiyoshi Matsui[3], Shoko Sakai[4] and Norio Yamamura[1]

1 Center for Ecological Research, Kyoto University, Ohtsu, Japan
2 Institute of Botany, Mongolian Academy of Science, Ulan Bator, Mongolia
3 Biological Laboratory, Nara University of Education, Nara, Japan
4 Research Institute for Humanity and Nature, Kyoto, Japan

**Keywords**
Plant coverage; plant growth; plant species richness; Simpson's index of diversity; Ulan Bator.

**Correspondence**
Noboru Fujita, Center for Ecological Research, Kyoto University, Ohtsu 520-2113, Japan.
Email: fujita@ecology.kyoto-u.ac.jp

*Present address*: Yasuhiro Yamada, Graduate School of Environmental Science, Okayama University, Japan.

*Present address*: Norio Yamamura, Research Institute for Humanity and Nature, Kyoto, Japan.

Received 9 January 2008;
accepted 15 April 2009.

doi: 10.1111/j.1744-697X.2009.00147.x

## Abstract

To examine different effects of herbivorous large mammals' grazing pressure on plant diversity along a slope in a Mongolian nomadic pasture, we compared species richness, Simpson's index of diversity, and the total plant coverage of plants between protected pasture from livestock grazing and grazed pasture on the near ridge, upper slope, lower slope, foot slope and valley bottom. The species richness and Simpson's index of diversity decreased and the total coverage increased downwardly with increase in pasture soil moisture along the slope. The species richness of the protected pasture decreased, changed little, and increased on the near ridge and the upper slope, the lower slope and the foot slope, and the valley bottom, respectively. Simpson's index of diversity of the protected pasture decreased compared with the grazed pasture only on the valley bottom. The total coverage became lower in the grazed pasture. As the reason for our results, we discuss positive and negative effects of livestock grazing on the species diversity of plants. The positive effect is shown on the valley bottom, where soil moisture and plant growth becomes high with the total coverage over 100%, due to relaxing indirectly the competitive exclusion among plants due to the grazing of dominant plants. The negative effect is obtained on the near ridge and the upper slope, where the soil moisture and the plant growth are low, because of elimination of some plants from the pasture by direct grazing damage.

## Introduction

Species diversity is generally affected by natural and artificial perturbations in various ecosystems. One of the most well-known patterns is that species diversity is maximized under intermediate strengths of perturbation, which the intermediate hypothesis had been proposed to account for (Levin and Paine 1974; Connell 1978; Pacala and Crawley 1992). Fujita *et al.* (2002) also showed that the intermediate grazing pressure of livestock maximizes species richness of plants in Mongolian pasture.

Recent more elaborated studies in grasslands, however, reported various patterns for effects of grazing pressure of herbivorous large mammals on plant species richness: positive effects (Collins *et al.* 2002; Bakker *et al.* 2003; Wilsey and Polley 2003; Pykälä 2004; Frank 2005), negative effects (Guo 2004; Hendricks *et al.* 2005), or little effects (Tracy and Sanderson 2000). As for different effects of the grazing pressure on plant species richness, Proulx and Mazmunder (1998) had proposed a hypothesis: plant species richness increases with an increased grazing pressure in nutrient-rich environments, while it decreases in nutrient-poor environments. Kondoh (2001) theoretically corroborated this scheme by a mathematical model but it is not fully examined whether the grazing pressure really causes different effects on plant species richness depending on the nutrient condition of habitats. Nutrient level and soil moisture showed similar effects on plant growth and nutrient uptake (Singh and Rao 2005). It is possible that an increased grazing pressure has different effects on plant species richness along a soil moisture gradient similar to a soil nutrient gradient. Soil moisture increases downward along the slope within a short distance in a secondary forest of the warm-temperate zone in Japan (Yanagisawa and Fujita 1999) and in a Colorado shortgrass steppe (Hook and Burke 2000). The similar soil moisture gradient may arise on a slope in Mongolian nomadic pasture.

We can compare effects of grazing on plant diversity among habitats with different soil moisture conditions along the ridge-valley gradient on a slope in a Mongolian nomadic pasture, where sheep and goats graze equally from the valley to the ridge, by comparison of pastures outside and inside the fence after experimental fencing which protects the livestock grazing along the slope.

In this paper, we examine effects of livestock grazing on the plant species richness in habitats with different soil moisture conditions along the slope from the ridge to the valley, by using experimental fences to exclude grazers. We also discuss the mechanism of different effects of livestock grazing on the plant species richness.

## Materials and methods

### Study site

For the study site, we selected a slope in a catchment area in the forest-steppe zone at Gachuurt near Ulan Bator, Mongolia. Annual precipitation of Gachuuurt was 280.5, 384.2 and 321.6 mm in 2000, 2001 and 2002, respectively. Monthly precipitation for the 3 years is shown in Figure 1 where

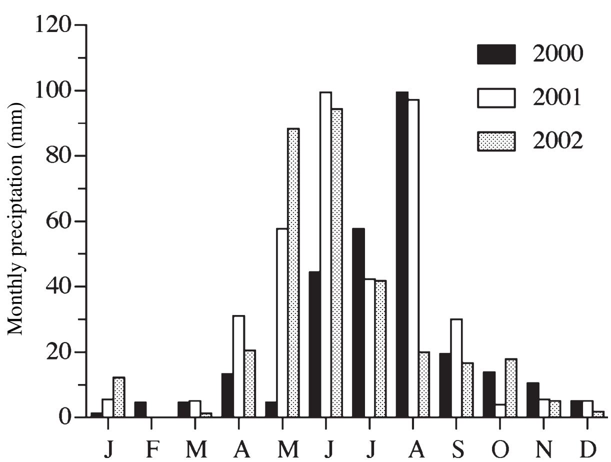


**Figure 1** Monthly precipitation from 2000 to 2002 at Gachuurt, Ulan Bator, Mongolia.

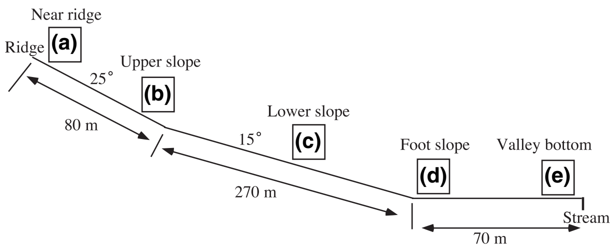


**Figure 2** A schematic cross-section of topography of the study site from the ridge to the streamside through the upper slope, lower slope and foot slope. (a–e) Position of each enclosure.

much rain fell in the summer. A stream flows only in spring from the north to the south in the flat valley bottom, and the slope faces the east in the lower reaches. The altitude of our site varies from 1550 m a.s.l. at the foot (48°00′74″N, 107°11′26″E) to 1650 m a.s.l. at the ridge of the slope (48°00′64″N, 107°11′01″E), and the distance between those positions is approximately 350 m a.s.l. The upper slope is steep with an inclination of 25° and the lower slope is gentler with the inclination of 15° (Figure 2). Two nomad families lived near the slope in the summer season, and each family had nearly 300 head of sheep and goats. Nearly 600 head of sheep and goats usually grazed the whole slope.

### Enclosure experiment

To examine the effects of grazing on diversity of the plants under different positions along the slope, five 8 m × 8 m square enclosures were set along the slope, at the near ridge position of the hill (1645 m a.s.l.), the upper slope of the hill (1620 m a.s.l.), the lower slope of the hill (1590 m a.s.l.), the foot of the hill (1550 m a.s.l.), and the flat valley bottom (1548 m a.s.l.) as control of the grazed pasture in the middle of July 2000 (Figure 2). We put each fence on a plane surface to make the soil moisture as homogeneous as possible within the fence. We fenced the experimental positions by pillars and rectangular lumbers to avoid excessive shading.

For the measurements described below, five 1 m × 1 m square quadrats were arbitrarily set both inside and outside each enclosure just before the fences were placed in 2000. The procedure was repeated in July 2001 and 2002. We could not take the measurements for the top position in 2002, because the enclosure was stolen during the winter of 2001.

For each quadrat, the maximum height of leaves and the coverage area of each plant species were recorded. Coverage of each species was calculated as the sum of areas occupied by individuals or patches of the species with a minimum of 0.1%. We calculated the total coverage of the quadrat as the sum of the coverage of each plant species, which sometimes exceeded 100%. We measured Simpson's index of diversity

(Simpson 1949) based on the coverage of each species instead of individual number in each quadrat.

To estimate the grazing pressure on the five positions, we compared the maximum heights of Gramineae and *Allium* species between inside and outside the enclosure. The species of Gramineae and *Allium* in this study site are all edible for livestock and grazing pressure of livestock can be estimated from the height of plants (Fujita *et al.* 2002). To estimate productivity of plants, we harvested plants at the height of 3 cm in five 1 m × 1 m square quadrats arbitrarily selected in the enclosure at each position, except for the top, on 10 August 2002. Five soil samples were collected from the depth of 10 cm just outside each enclosure on 13 July 2002, and the soil water potential was measured using a psychrometer (WP4; Decagon Devices, Pullman, WA, USA).

We used Tukey's honestly significant difference test for the mean comparison of the five samples of plant height, soil water potential, species richness, Simpson's index of diversity and total coverage. These statistical analyses were performed using JMP for Macintosh, ver. 5.1.2.

To assess variation in the major species composition of the plants inside and outside of the enclosures at the five positions, we conducted principal components analysis (PCA) using the coverage of 11 major plant species that occurred in 20 or more 1 m × 1 m quadrats with more than 1% of the coverage. The coverage of the plants in the five quadrats inside and outside of the enclosure in each position were averaged to obtain 10 vegetation samples for PCA.

We also used a three-way ANOVA to test the effects of grazing, positions along the slope, years (2001 and 2002) and their interactions on plant species diversity and coverage. For species diversity, natural log transformations were performed on the Simpson's index of diversity to satisfy the assumption of the analysis of normality and equal variances. Species richness (the numbers of the species) was not included in the analysis, because the variable did not satisfy the assumption. To avoid the problem of the missing cell, we exclude data of plot a. The analysis was conducted using R (R Development Core Team 2008).

Nomenclature follows Grubov (2001) except for *Leymus chinensis*. *L. chinensis* based on Gubanov (1996).

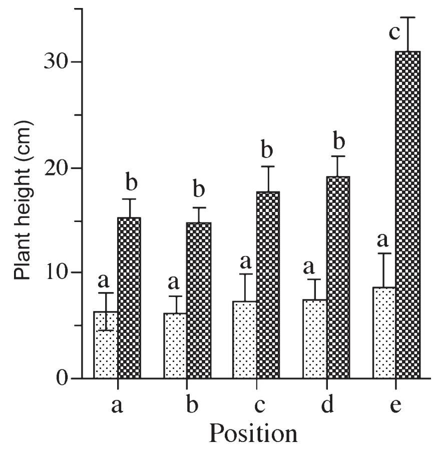


**Figure 3** The average plant height with standard error at each position. Light and dark bars are grazed and protected pastures, respectively. (a–e) Near ridge, upper slope, lower slope, foot slope and valley bottom, respectively. The different letters in the panel show significant difference between averages ($P < 0.05$).

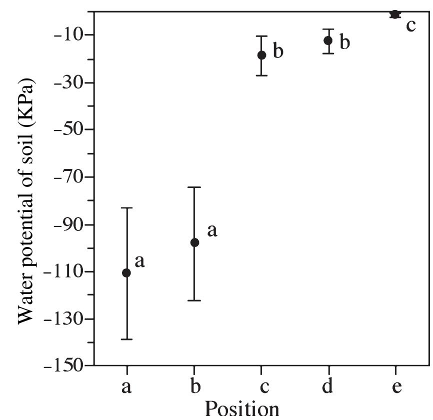


**Figure 4** The average soil water potential with standard error at each position. (a–e) Near ridge, upper slope, lower slope, foot slope and valley bottom, respectively. The different letters in the panel show significant difference between averages ($P < 0.05$).

## Results

### Grazing pressure, soil water potential and productivity

There were significant differences in the height of pasture plant species of Gramineae and *Allium* between outside and inside the fences. The grazed height that may indicate grazing pressure was not significantly different among outside the fences in all positions (Figure 3). The study site had an ascending gradient of soil moisture along a slope from the ridge to the valley (Figure 4). According to the soil moisture, the experimental positions can be divided into three groups: the lowest of the ridge and upper slope; the intermediate of the lower slope and foot slope; and the highest of the valley bottom. The standing crop of plants above 3 cm was the lowest on the upper slope and the highest on the valley bottom among four positions (Figure 5).

### Vegetation pattern

Species occurrence on each position in 2001 is shown in the Appendix. PCA of 11 major plant species showed the vegetation on the slope can be two-dimensionally classified into

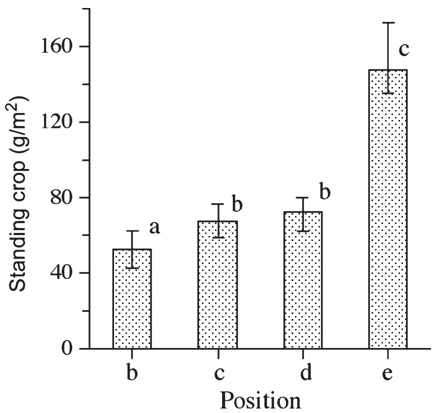


**Figure 5** The average standing crop of plants above 3 cm with standard error in the enclosure at each position in 2002. (b–e) Positions of the upper slope, lower slope, foot slope and valley bottom, respectively. The different letters in the panel show significant difference between averages ($P < 0.05$).

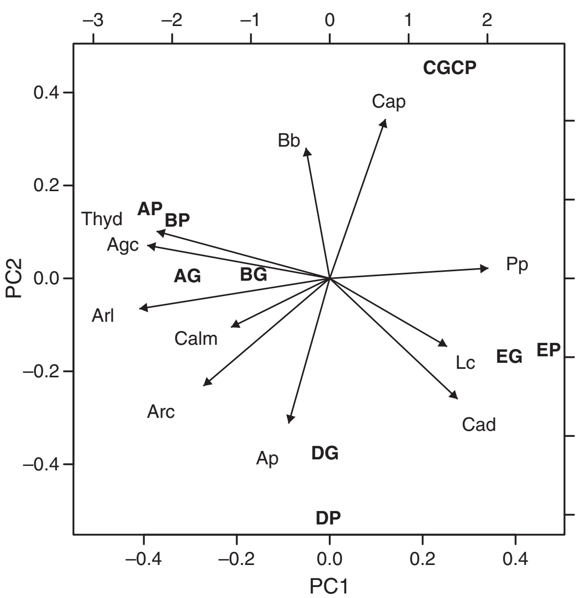


**Figure 6** Principal components analysis (PCA) using the coverage of 11 major plant species. Bold letters mean the pasture: A, near ridge; B, upper slope; C, lower slope; D, foot slope; and E, valley bottom; P, protected; and G, grazed. Agc, *Agropyron cristatum*; Ap, *Allium prostratum*; Arc, *Arenalia capillaris*; Arl, *Artemisic laciniata*; Bb, *Bupleurum bicaure*; Cad, *Carex duriuscula*; Calm, *Calamagrostis macilenta*; Cap, *Carex pediformis*; Lc, *Leymus chinensis*; Pp, *Poa pratensis*; Thyd, *Thymus dahuricus*.

four groups: ridge and upper slope; lower slope; foot slope; and valley bottom (Figure 6). According to the first principal component that explains 42% of variation, ridge (AP and AG), valley (EP and EG) gradient of vegetation occurred. According to the second principal component that explains 23% of variation, the lower slope vegetation (CP and CG) and the foot slope vegetation (DP and DG) were divided.

## Effects of grazing on plant diversity and coverage

Enclosure protection from grazing had different effects on plant species richness of a pasture at different positions on the slope, from the ridge to the valley bottom (Figure 7). On the near ridge and the upper slope that are higher positions, the plant species richness was significantly lower in the grazed pasture than in the protected pasture, while, on the valley bottom that is the lowest position, it was significantly higher in the grazed pasture than in the protected pasture. On the lower slope and the foot slope that are middle positions, there was no difference between the grazed pasture and the protected pasture. As for yearly changes of the species richness of plants, it tended to become high in 2001 and lowest in 2000 with little significance.

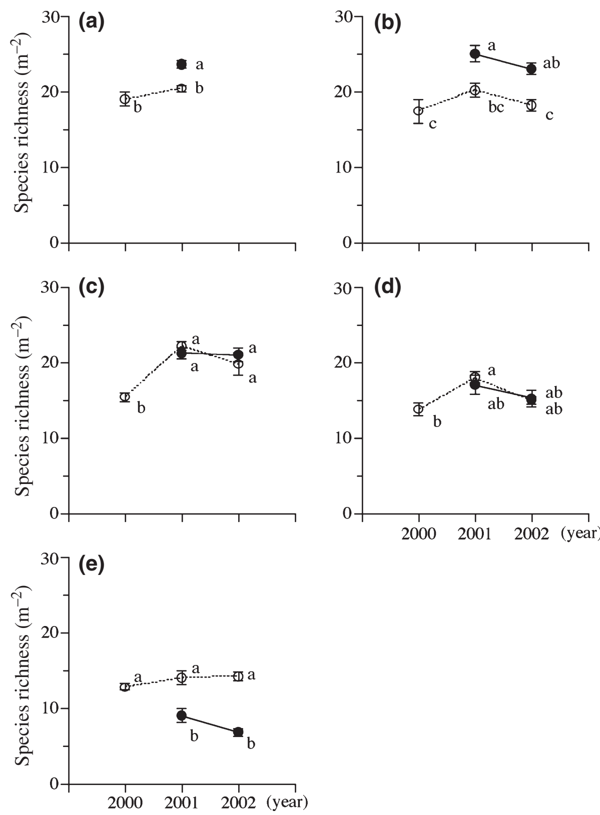


**Figure 7** The average plant species richness with standard error at each position. White and black circles are the grazed and protected pastures, respectively. (a–e) Positions of the near ridge, upper slope, lower slope, foot slope and valley bottom, respectively. The different letters in each panel show significant difference between averages ($P < 0.05$).

Plant species that occurred in not less than two quadrats only in the protected pasture or in the grazed pasture on the near ridge, the upper slope and the valley bottom are listed in Table 1. On the near ridge and upper slope where plant species richness increased in the protected pasture, plant species that occurred only in the protected pasture predominated over those that occurred only in the grazed pasture. They are edible for livestock except for *Stellera chamajasme* that is strongly toxic. Those that were found only in the grazed pasture are almost grazing-tolerant. *Astragalus mongolicus* is edible but creeping, and it may become escape from grazing. On the valley bottom where plant species richness decreased in the protected area, plant species that occurred only in the grazed pasture predominated over the species that was found in the protected pasture. They are mainly escape plants that are able to avoid livestock grazing due to low height. *Equisetum arvense* is grazing-tolerant. *Bromus inermis* is an exception, because it can become large and is edible. *Vicia costata* that grew only in the protected pasture is edible.

The enclosure protection from livestock grazing exhibited significant effect on Simpson's index of diversity of plants (Figure 8) only at the valley bottom. Simpson's index of diversity of the protected pasture was significantly lower than that of the grazed pasture at the valley bottom. Yearly differences of Simpson's index of diversity in the grazed pasture were clearer than that of the species richness. Simpson's index of diversity of the grazed pasture was significantly lowest in 2000 among 3 years, on all positions excepting on the lower slope. ANOVA suggested the most important determinant for the index was the position on the slope. Highly significant effect of interaction between grazing and position, and less significantly between year and grazing, were also detected, suggesting that effects of grazing and yearly

**Table 1** Species that occurred only in the enclosure or out of the enclosure on the near ridge, the upper slope and the valley bottom with the number of appeared quadrats out of five

| Position | Year | Enclosure | No. of quadrats | Species name |
|---|---|---|---|---|
| a | 2001 | In | 3 | *Dontosemon integrifolius* |
| a | 2001 | In | 2 | *Poa pratensis* |
| a | 2001 | Out | 2 | *Astragalus mongolicus* |
| b | 2001 | In | 2 | *Allium odorum* |
| b | 2001 | In | 2 | *Linaria acutiloba* |
| b | 2001 | In | 2 | *Poa pratensis* |
| b | 2001 | In | 4 | *Pulsatilla ambigua* |
| b | 2001 | In | 3 | *Stellera chamajasme* |
| b | 2001 | In | 3 | *Stipa krylovii* |
| b | 2002 | In | 2 | *Androsace septentrionalis* |
| b | 2002 | In | 4 | *Artemisia frigida* |
| b | 2002 | In | 5 | *Chamaerhodos erecta* |
| b | 2001 | Out | 2 | *Caragana leucophloea* |
| b | 2001 | Out | 2 | *Leonthopodium leonthopodoides* |
| b | 2002 | Out | 2 | *Peusedanom hystrix* |
| e | 2001 | In | 2 | *Vicia costata* |
| e | 2001 | Out | 3 | *Bromus inermis* |
| e | 2001 | Out | 4 | *Equisetum arvense* |
| e | 2001 | Out | 5 | *Mentha arvensis* |
| e | 2001 | Out | 2 | *Plantago depressa* |
| e | 2001 | Out | 2 | *Potentilla multifida* |
| e | 2001 | Out | 3 | *Taraxacum bornuurense* |
| e | 2002 | Out | 2 | *Circium esculantum* |
| e | 2002 | Out | 2 | *Glaux maritima* |
| e | 2002 | Out | 5 | *Halerpestes salsuginosa* |
| e | 2002 | Out | 5 | *Mentha arvensis* |
| e | 2002 | Out | 2 | *Plantago depressa* |
| e | 2002 | Out | 3 | *Taraxacum bornuurense* |
| e | 2002 | Out | 2 | *Trifolium lupinaster* |

a, the near ridge; b, the upper slope; e, the valley bottom.

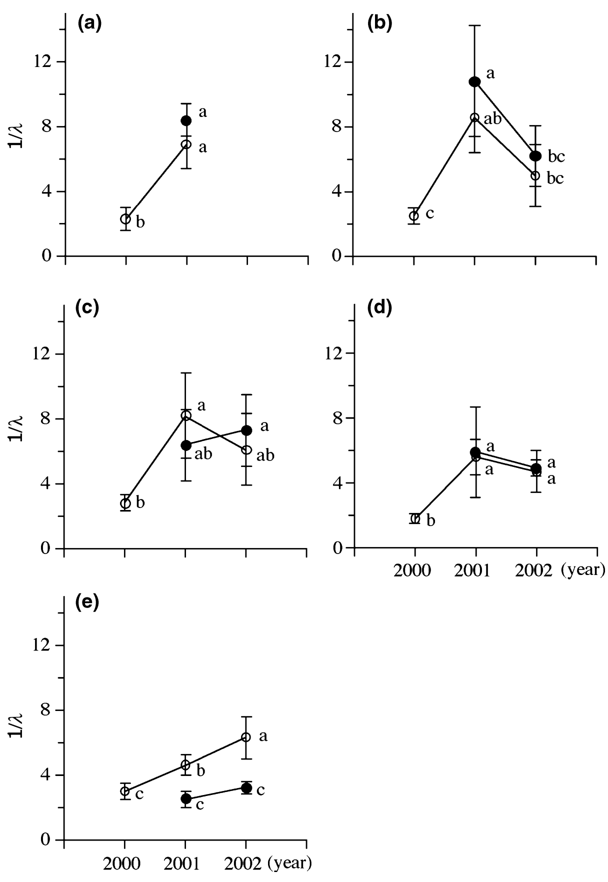


**Figure 8** The average of Simpson' index of diversity ($1/\lambda$) with standard error at each position. White and black circles are the grazed and protected pastures, respectively. (a–e) Positions of the near ridge, upper slope, lower slope, foot slope and valley bottom, respectively. The different letters in each panel show significant difference between averages ($P < 0.05$).

**Table 2** ANOVA tables for the experiment examining grazing effects at different positions on the slope

| Source | d.f. | SS | *F* | *P* |
|---|---|---|---|---|
| (a) Simpson's index of diversity | | | | |
| Year | 1 | 0.40 | 5.2 | **0.0260** |
| Grazing | 1 | 0.17 | 2.3 | 0.1359 |
| Position | 3 | 4.56 | 19.9 | **<0.0001** |
| Year × grazing | 1 | 0.06 | 0.8 | 0.3811 |
| Year × position | 3 | 1.72 | 7.5 | **0.0002** |
| Grazing × position | 3 | 2.24 | 9.8 | **<0.0001** |
| Three-way interaction | 3 | 0.18 | 0.8 | 0.5186 |
| Residuals | 64 | 4.89 | | |
| (b) Total coverage | | | | |
| Year | 1 | 2238 | 27.2 | **<0.0001** |
| Grazing | 1 | 6902 | 84.0 | **<0.0001** |
| Position | 3 | 51829 | 210.2 | **<0.0001** |
| Year × grazing | 1 | 0 | 0.0 | 0.9951 |
| Year × position | 3 | 133 | 0.5 | 0.6568 |
| Grazing × position | 3 | 1071 | 4.3 | **0.0075** |
| Three-way interaction | 3 | 124 | 0.5 | 0.6818 |
| Residuals | 64 | 5260 | | |

Significant *P*-values are highlighted.

variation on the diversity index were quite variable among positions (Table 2a).

The total coverage of plants was lower in the grazed pasture than in the protected pasture at all the positions in all study years, although significant differences were only observed on the higher slope of 2002, the lower slope of 2001, and the valley bottom of both 2001 and 2002 (Figure 9). It did not exceed 100% except for the valley bottom. On the valley bottom, it was nearly 100% in the grazed pasture and far over 100% in the protected pasture where many individual plants overlapped each other. In all positions, the total coverage was highest in 2001 among the observed years. ANOVA showed that the total coverage was mostly explained by the main effect of position, followed by grazing and year. Significant but relatively minor effect was also detected for interaction between grazing and position (Table 2b).

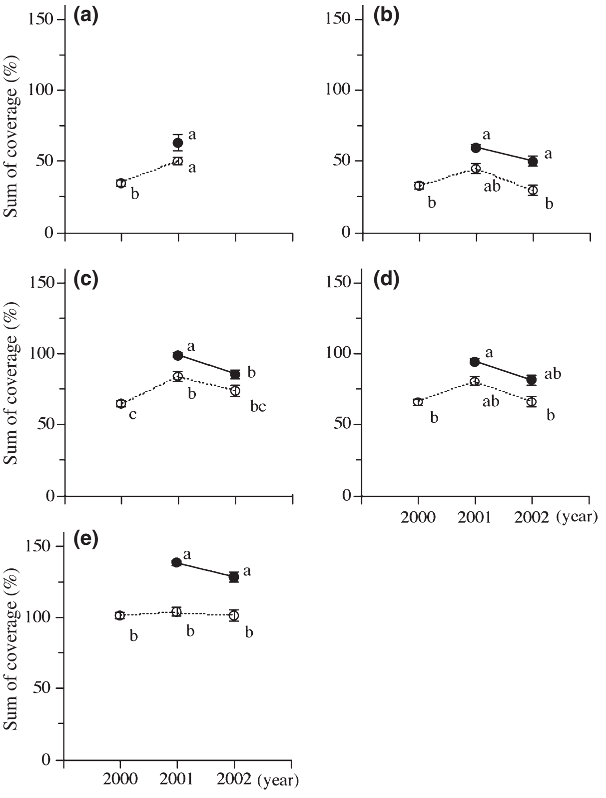


**Figure 9** The average total plant coverage with standard error at each position. White and black circles are the grazed and protected pastures, respectively. (a–e) Positions of the near ridge, upper slope, lower slope, foot slope and valley bottom, respectively. The different letters in each panel show significant difference between averages ($P < 0.05$).

## Discussion

Our results meant that, when we protected the grazed pasture by fencing from livestock grazing, species richness of plants decreased, changed little, and increased on the valley bottom with high soil moisture, on the lower slope and foot slope with intermediate soil moisture, and on the near ridge and upper slope with low soil moisture, respectively. These different effects of livestock grazing on the diversity of plants were also detected as a highly significant effect of the interaction between grazing and position for Simpson's index of diversity in ANOVA (Table 2a) This means that the livestock grazing can increase and decrease the plant species diversity under high soil moisture conditions and under low soil moisture conditions, respectively, under conditions of grazing pressure and soil moisture in our study site. These changes in the plant species diversity between the protected pasture and the grazed pasture may be caused by presence and absence of minor plant species, because PCA of the 11 major plant species (Figure 6) showed that coordinates were little different between the protected pasture and the grazed pasture at each position. What is the mechanism leading to our results?

Among the protected plots, plant species richness was the lowest at the valley bottom pasture among all positions. In the valley bottom pasture, soil water potential (Figure 4) and standing crop (Figure 5) showed the highest. The total plant coverage of the protected pasture exceeded 100% on the valley bottom (Figure 9). When Simpson' index of diversity of plants is compared between the grazed pasture and the protected pasture in each position, significant difference was found only on the valley bottom, and it became lower in the protected pasture than that in the grazed pasture (Figure 8). Then, dominant plant species occurred at the valley bottom under protected condition, suggesting that fast plant growth intensified plant competition. Along the slope, species richness (Figure 7) and Simpson' index of diversity (Figure 8) of plants decreased downwardly with increase in plant growth (Figure 5), the total coverage of plants (Figure 9) and the soil moisture of the pasture (Figure 4). The decrease of plant species richness might be brought about by the competitive exclusion among plants, which is suggested by previous studies (Newman 1973; Goldberg and Miller 1990; Rebele 2000; Rajaniemi 2003).

The livestock grazing that reduced the total coverage to nearly 100% in the grazed pasture on the valley bottom might be effective enough to increase the species richness by lowering the strong plant competition possibly for light. This is supported by the fact that plant species that grew only in the grazed pasture and contributed to the increase in the species richness of the grazed pasture on the valley bottom in 2001 are almost escape plants with low height (Table 1).

On the other hand, in the pastures on the near ridge and upper slope, plant species richness in the protected pasture became higher than that in the grazed pasture (Figure 7). Removal of the plants by livestock grazing causes not only possible easing of plant competition due to improvement of light environment but also direct damage to the plants. The improvement of light environment by livestock grazing might become negligible in the pastures that had low total coverage of plants far below 100% (Figure 9). But, the grazed damage of the plants becomes severer as the growth rate of plants is low on the upper slope (Figure 5) due to the low level of habitat soil moisture (Figure 4). Increased plant species richness in the protected pasture on the near ridge and upper pastures in 2001 and 2002 may be produced by recovery of some plants that was eliminated in the grazed pasture in 2000 due to the grazing damage. Therefore, the plant species richness of plants became increased by the protection from the livestock grazing on the near ridge and the upper slope. This is supported by the fact that plant species that occurred only in the protected pasture and contributed to the increase in the species richness of the protected pasture on the near ridge and the upper slope in 2001 are almost edible plants for livestock (Table 1).

On the lower slope and the foot slope with the intermediate soil moisture and standing crop of plants, the species richness of plants did change a little by the protection from the livestock grazing. This little change could be possible if negative effect of direct damage and positive effect of easing of plant competition on plant species richness balanced synergistically.

Along a slope, soil nutrients usually increase downward (Schimel *et al.* 1985; Hook and Burke 2000; Li *et al.* 2006) like soil moisture. Plant species diversity decreases as habitat fertility becomes high (Wilson and Tilman 1991; Campbell and Grime 1992; Rajaniemi 2002). This is because of greater competitive exclusion among plants at high productivity (Rajaniemi 2003), though good nutrient supply itself in the nutrient-rich habitat relaxes plant competition for nutrients (Huston and DeAngelis 1994). Positive and negative effects of livestock grazing on plant species diversity can be produced along the soil moisture gradient and the correlated soil nutrient gradient. Proulx and Mazmunder (1998) hypothesized that plant species richness increases with an increased grazing pressure in nutrient-rich environments, while it decreases in nutrient-poor environments. It is possible that the grazing pressure shows the same effects on the plant species richness both along the soil moisture and nutrient gradients, because both sufficient soil moisture and sufficient nutrients increase plant growth and both poor soil moisture and poor nutrients decrease plant growth.

In conclusion, the livestock grazing has different two effects on plants along a slope with soil moisture gradient. On the near ridge and the upper slope with low soil moisture, the livestock grazing has a negative effect caused by direct damage to plants, which is capable of eliminating some plant species from the pasture. On the valley bottom with high soil moisture, it shows a positive effect by relaxing indirectly the competitive exclusion among plants probably due to the improvement of light environment. We suggest that different effects are brought about by different growth conditions under the soil moisture gradient.

## Acknowledgments

We would like to thank Dr E. Wada (FRCGC, JAMSTEC), Dr C. Dugarjav (Institute of Botany, Mongolian Academy of Science) and Dr J. Tsogtbaatar (Institute of Geoecology, Mongolian Academy of Science) for their kind assistance and advice. This work was financially supported in part by RIHN research project "Collapse and Restoration of Ecosystem Networks with Human Activities" and the Global COE Program A06 to Kyoto University.

## References

Bakker C, Blair JM, Knapp AK (2003) Does resource availability, resource heterogeneity or species turnover mediate changes in plant species richness in grazed grasslands? *Oecologia* 137: 385–391.

Campbell BD, Grime JP (1992) An experimental test of plant strategy theory. *Ecology* 73: 15–29.
Collins SL, Glenn SM, Briggs JM (2002) Effect of local and regional processes on plant species richness in tall grass prairie. *Oikos* 99: 571–579.
Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199: 1302–1310.
Frank DA (2005) The interactive effects of grazing ungulates and aboveground production on grassland diversity. *Oecologia* 143: 629–634.
Fujita N, Amartuvshin N, Uchida T, Wada E (2002) Biodiversity and sustainability of Mongolian herbaceous plants subjected to nomadic grazing. In: *Sustainable Watershed with Emphasis on Lake Ecosystems* (Eds Fujita N *et al.*), DIWPA Series 3, Nauka-Center, Novosibirsk, 101–107.
Goldberg DE, Miller TE (1990) Effects of different resource additions on species diversity in an annual plant community. *Ecology* 71: 213–225.
Grubov VL (2001) *Key to the Vascular Plants of Mongolia Vol. I and Vol. II*. Science Publishers, Enfield, 1–817.
Gubanov IA (1996) *Conspectus of Flora of Outer Mongolia (vascular plants)*. Valang Publusher, Moscow, 1–132.
Guo Q (2004) Slow recovery in desert perennial vegetation following prolonged human disturbance. *J Veg Sci* 15: 757–762.
Hendricks HH, Bond WJ, Midgley JJ, Novellie PA (2005) Plant species richness and composition a long livestock grazing intensity gradients in a Namaqualand (South Africa) protected area. *Plant Ecol* 176: 19–33.
Hook PB, Burke IC (2000) Biogeochemistry in a shortgrass landscape: control by topography, soil texture, and microclimate. *Ecology* 81: 2686–2703.
Huston MA, DeAngelis DL (1994) Competition and coexistence: the effects of resource transport and supply rates. *Am Nat* 144: 954–977.
Kondoh M (2001) Unifying the relationships of species richness to productivity and disturbance. *Proc R Soc Lond Ser B* 268: 269–271.
Levin SA, Paine RT (1974) Disturbance, patch formation, and community structure. *Proc Natl Acad Sci USA* 71: 2744–2747.
Li Y, Wang C, Tang H (2006) Research advances in nutrient runoff on sloping land in watersheds. *Aquat Ecosystem Health and Manag* 9: 27–32.
Newman EI (1973) Competition and diversity in herbaceous vegetation. *Nature* 244: 310.
Pacala SW, Crawley MJ (1992) Herbivores and plant diversity. *Am Nat* 140: 243–260.
Proulx M, Mazmunder A (1998) Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* 79: 2581–2592.
Pykälä J (2004) Cattle grazing increases plant species richness of most species trait groups in mesic semi-natural grasslands. *Plant Ecol* 175: 217–226.
R Development Core Team (2008) *R: A Language and Environment for Statistical Computing* Version 2.8.1. R Foundation for Statistical Computing, Vienna, Austria, available from URL: http://www.r-project.org/ [cited 20 November 2008].
Rajaniemi TK (2002) Why does fertilization reduce plant species diversity? Testing three competition-based hypotheses. *J Ecol* 90: 316–324.
Rajaniemi TK (2003) Explaining productivity-diversity relationships in plants. *Oikos* 101: 449–457.
Rebele F (2000) Composition and coexistence of rhizomatous perennial plants along a nutrient gradient. *Plant Ecol* 147: 77–94.
Schimel DS, Stillwell MA, Woodmansee RG (1985) Biogeochmistry of C, N, and P in a soil catena of the shortgrass steppe. *Ecology* 66: 275–282.
Simpson EH (1949) Measurement of diversity. *Nature* 163: 688.
Singh M, Rao RSG (2005) Effects of nitrogen, potassium and soil moisture regime on growth, herbage, oil yield and nutrient uptake on South American marigold (*Tagetes minuta* L.) in a semi-arid tropical climate. *J Hortic and Sci Biotechnol* 80: 488–492.
Tracy BF, Sanderson MA (2000) Patterns of plant species richness in pasture lands of the northeast United States. *Plant Ecol* 149: 169–180.
Wilsey BJ, Polley HW (2003) Effects of seed additions and grazing history on diversity and productivity of subhumid grasslands. *Ecology* 84: 920–931.
Wilson SD, Tilman D (1991) Components of plant competition along an experimental gradient of nitrogen availability. *Ecology* 72: 1050–1065.
Yanagisawa N, Fujita N (1999) Different distribution patterns of woody species on a slope in relation to vertical root distribution and dynamics of soil moisture profiles. *Ecol Res* 14: 165–177.

## Appendix

### Occurrence of each species in each position is shown by x

| | Position | | | | |
|---|---|---|---|---|---|
| Species name | a | b | c | d | e |
| *Agropyron cristatum* (L.) P. B. | x | x | x | x | |
| *Allium odorum* L. | x | | | x | |
| *Allium prostratum* Trev. | x | x | x | x | |
| *Alyssum lenense* Adams | x | x | x | | |
| *Androsace septentronalis* L. | x | x | x | x | |
| *Arenalia capillaris* Poir. | x | x | x | x | |
| *Artemisia dolosa* Krasch. | x | | | x | |
| *Artemisia dracunculus* L. | | | x | x | |
| *Artemisia frigida* Wild. | x | x | | x | |
| *Artemisia laciniata* Wild. | x | x | x | x | |
| *Aster alpinus* L. | x | x | | | |
| *Astragalus adsurgens* Pall. | | x | | x | |

## Appendix *(Continued)*

| Species name | Position a | b | c | d | e |
|---|---|---|---|---|---|
| *Astragalus mongolicus* Bge. | | | x | x | |
| *Bromus inermis* Leyss. | | | x | | x |
| *Bupleurum bicaule* Helm. | x | x | x | x | |
| *Calamogrostis macilenta* (Griseb.) Litv. | x | x | x | x | x |
| *Caragana leucophloea* Pojark. | x | x | x | | |
| *Caragana microphylla* (Pall.) Lam. | | | x | | |
| *Carex duriuscula* C. A. Mey. | | | | x | x |
| *Carex pediformis* C. A. Mey. | x | x | x | | |
| *Carum buriaticum* Turcz. | x | x | x | x | |
| *Carum carvi* L. | | | | | x |
| *Chamaerhodos erecta* (L.) Bunge | | x | | | |
| *Circium esculentum* (Siev.) C. A. Mey. | | | | | x |
| *Cleistogenes squarrosa* (Trin.) Keng | | | | x | |
| *Delphinium cheilanthum* Fisch. | | | x | | |
| *Dianthus versicolor* Fisch. | x | x | x | | |
| *Dontostemon integrifolius* (L.) C. A. Mey. | x | x | | x | |
| *Draba nemorosa* L. | x | x | | | |
| *Echinops latifolius* Tausch | | | x | | |
| *Ephedra sinica* Stapf | x | | | | |
| *Equisetum arvense* L. | | | | | x |
| *Filifolium sibiricum* (L.) Kitam. | x | | x | x | |
| *Galium verum* L. | | x | x | | |
| *Gentiana decumbens* L. f. | | | x | | |
| *Gentiana squarrosa* Lab. | | | | x | |
| *Geranium pratense* L. | | | x | | |
| *Glaux maritima* L. | | | | | x |
| *Goniolimon speciosum* (L.) Boiss. | | x | | | |
| *Halerpestes salsuginosa* (Pall. ex Georgi) Greene | | | | | x |
| *Heteropappus altaicus* (Wild.) Novopokr. | x | x | x | x | |
| *Hordeum brevisubulatum* (Trn.) Link | | | | | x |
| *Iris tigrida* Bge. | x | x | x | x | |
| *Lathyrus humilis* (Ser.) Spreng. | x | x | | | |
| *Leontopodium leontopodoides* (Wild.) Beauvd. | x | x | x | x | |
| *Leuzea uniflora* (L.) Holub | | x | | | |
| *Leymus chinensis* (Trin.) Tzvel. | | x | x | x | x |
| *Linaria acutiloba* Fisch. ex Reichb. | | x | x | | |
| *Mentha arvensis* L. | | | x | | x |
| *Myosotis caespitosa* C. F. Schultz. | | | x | x | |
| *Nepeta sibirica* L. | | | x | | |
| *Orostachys spinosa* (L.) C. A. Mey. | x | x | x | | |
| *Oxytropis filiformis* DC. | x | x | | x | |
| *Oxytropis strobilacea* Bge. | | x | x | | |

## Appendix *(Continued)*

| Species name | Position a | b | c | d | e |
|---|---|---|---|---|---|
| *Papaver nudicaule* L. | x | x | | | |
| *Pedicularis tristis* L. | x | | | | |
| *Peucedanum hystrix* Bge. | x | x | | | |
| *Phlomis tuberosa* L. | | | x | | |
| *Plantgo depressa* Wild. | | | x | x | x |
| *Poa pratensis* L. | x | x | x | x | x |
| *Polygala tenuifolia* Wild. | | x | | | |
| *Polygonum angustifolium* Pall. | x | x | x | | |
| *Polygonum aviculare* L. | | | | | x |
| *Polygonum sibiricum* Laxm. | x | | x | | |
| *Potentilla acaulis* L. | | x | x | x | |
| *Potentilla anserina* L. | | | | | x |
| *Potentilla astragalifolia* Bge. | x | x | x | x | |
| *Potentilla bifurca* L. | | | x | x | |
| *Potentilla multifida* L. | | | | | x |
| *Pulsatilla ambigua* (Turcz.) Juz. | x | x | | x | x |
| *Ranunculus japonicus* Thunb. | | | | | x |
| *Ranunculus repens* L. | | | | | x |
| *Rheum compactum* L. | | | x | | |
| *Sanguisorba officinalis* L. | | | | | x |
| *Scabiosa comosa* Fisch. | | | x | | |
| *Scutellaria scordifolia* Fisch. ex Schrank | | | x | | |
| *Serratula marginata* Tausch | x | x | x | x | |
| *Sibbaldianthe adpressa* (Bge.) Juz. | | x | x | x | |
| *Silene repens* Patr. | x | x | x | x | |
| *Stellaria dichotoma* L. | x | x | | | x |
| *Stellaria petraea* Bge. | x | x | | | |
| *Stellera chamaejasme* L. | x | x | x | | |
| *Stipa krylovii* Roshev. | | x | x | x | |
| *Taraxacum bornuurense* Doll | | | | | x |
| *Taracacum collinum* DC. | x | x | | x | |
| *Taraxacum leucanthum* (Ldb.) Ldb. | | x | x | x | |
| *Thalictrum foetidum* L. | | x | x | | |
| *Thalictrum simplex* L. | | | x | | |
| *Thermopsis dahurica* Czefr. | | | x | | |
| *Thesium refractum* C. A. Mey. | | | x | | |
| *Thymus dahuricus* Serg. | x | x | x | | |
| *Tragopogon trachycarpus* S. Nikit. | | | | x | |
| *Trifolium lupinaster* L. | | | x | | x |
| *Urtica angustifolia* Fisch. ex Hornem. | | | x | | |
| *Veronica incana* L. | | | | x | |
| *Vicia costata* Ldb. | | | x | | x |
| *Youngia tenuifolia* (Wild.) Babs. et Stebbins | x | x | x | | |