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Changes in the herbage nutritive value and yield associated with threshold responses of vegetation to grazing in Mongolian rangelands

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Abstract

We examined the changes in the nutritive value and yield of herbage along a grazing gradient, where abrupt changes in community composition occurred, at multiple ecological sites in Mongolian rangelands. At grassland sites, changes in the herbage nutritive value could be attributed to rapid replacement of perennial grasses or forbs with weedy annual forbs along a grazing gradient. Crude protein (CP) concentration increased sharply in approaching the source of grazing gradient, whereas neutral detergent fibre and metabolizable energy (ME) concentrations decreased sharply. As ME can be utilized as a main index of herbage nutritive value, these results indicated its overall loss with severe grazing. Consequently, gradual increases in the yields of CP and ME in the direction of the gradient source at the grassland sites did not necessarily indicate the improvement of rangeland condition. In contrast, at shrubland sites, we could not generally detect any significant trends in the herbage nutritive value. The yield of ME gradually decreased in the direction of gradient source, suggesting that grazing affects herbage yield rather than herbage feed value at shrubland sites. Thus, the nutritive value and yield of herbage can be modified greatly in association with nonlinear responses of vegetation to livestock grazing.

Keywords: arid and semi-arid rangelands, ecological threshold, ecosystem services, forage resources, rangeland management

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Introduction

Global environmental changes, including land-use and land cover changes, have considerable impacts on the ecological properties of ecosystems and therefore on the ecosystem services that societies derive from them (Millennium Ecosystem Assessment, 2005). Ecosystem services are a set of ecological processes required for sustained social and ecological functioning and human activities (Costanza *et al.*, 1997). There is compelling evidence that current patterns of natural resource consumption are depleting the capacity for the future production of ecosystem services (Tilman *et al.*, 2002; Wackernagel *et al.*, 2002).

The diminishing rate of production of many ecosystem services can be linked to anthropogenic alterations in ecosystems. Human activities in arid and semi-arid ecosystems rely upon local forage resources; the nutritional value of forage resources is important for raising healthy livestock and thereby maintaining sustainable production (DeYoung *et al.*, 2000; Briske *et al.*, 2008). The degradation of ecosystems caused by inappropriate management is particularly likely in arid and semi-arid regions (Briske *et al.*, 2003), and the impacts of severe livestock grazing on vegetation dynamics might lead to marked reductions in the nutritive value and yield of herbage (Chaneton *et al.*, 1988; Ayantunde *et al.*, 1999; Gutman *et al.*, 1999). On the other hand, grazing intensity can also affect herbage nutritive value positively as green and leafy herbage is maintained under some moderate level of herbivory (De Santis *et al.*, 2004; Henkin *et al.*, 2011). In this context, management strategies should be developed to sustain nutritive value as well as nutritive yield of herbage, and consequently to increase rangeland condition and animal production (Briske *et al.*, 2008).

Our work in Mongolian rangelands suggests the existence of an ecological threshold, which has been defined as the point or zone at which the value of

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some ecological parameters begins to change nonlinearly; thus, disturbance should be limited to values less than this threshold to avoid irreversible degradation of the ecosystem (Sasaki *et al.*, 2008a). In previous research, changes in community composition along a gradient of livestock grazing have been shown to exhibit a threshold response (Sasaki *et al.*, 2008a). However, we know little about the consequences of threshold responses of community composition to grazing in terms of the nutritional value and yield of plant communities. Observations of the modification of ecosystem services by human activities would be essential to the decision-making process in rangeland management.

Nutritive value of herbage depends on the ratio of positive (e.g. protein, fat) to neutral or negative (e.g. fibre, lignin) nutrients. Herbage of good quality would generally be one with high crude protein content, high calorific value and low fibre, lignin and ash contents (Van Soest, 1994). However, we cannot assess rangeland condition according to the absolute values of nutrient contents of plant communities across landscapes, because the nutrients differ according to the prevailing vegetation type at any site (Beeri *et al.*, 2005; Skidmore *et al.*, 2010). Moreover, the magnitude of responses by plant communities to grazing also differs according to vegetation type (Sasaki *et al.*, 2008b) and should be reflected in changes in the nutritive value of herbage along a grazing gradient. As the overall nutritive value of herbage would not necessarily directly contribute to nutritive value of diet of grazed livestock because of their ability to selectively graze plants, we also need to consider relative palatability of dominant species to livestock in communities. Thus, the assessment of rangeland condition according to the herbage nutritive value and yield should be based on changes in nutrients associated with changes in community composition along a grazing gradient at the local scale.

Here, we report the changes in the nutritive value and yield of herbage associated with threshold changes in community composition along grazing gradients from livestock camps or sources of water, representing a spatial gradient in the accumulated impact of long-term exposure to livestock (Andrew, 1988). In the direction of the source of grazing gradient, vegetation changed drastically from dominance by perennial grasses or forbs toward dominance by unpalatable forbs or weedy annuals at the grassland sites, or from dominance by shrub toward non-vegetated state at the shrubland sites (Sasaki *et al.*, 2008a). Thus, our focus in this study was to examine how these vegetation changes are reflected in variations in the nutritive value and yield of herbage along a grazing gradient in Mongolian rangelands.

Material and methods

Study areas and ecological sites

We selected three study areas in Mongolia: near Kherlen Bayan Ulaan, Khenti province (47°12′N, 108°44′E); near Mandalgobi, Dundgobi province (45°46′N, 106°16′E); and near Bulgan, South Gobi province (44°05′N, 103°32′E) (Table 1). The region's climate is arid and cold, with a short summer. The study areas have a long history of grazing by domestic livestock under nomadic or semi-nomadic patterns of land use. Herders raise sheep, goats and cattle in Kherlen Bayan Ulaan and Mandalgobi, and sheep, goats and camels in Bulgan. Although detailed information on livestock composition was not available, mainly sheep and goats are raised at each study site. According to Mongolia's Institute of Meteorology and Hydrology, Ministry of Nature and Environment, the annual rainfall averaged around 210 mm (coefficient of variation = 21%) at Kherlen Bayan Ulaan, 170 mm (28%) at Mandalgobi and 140 mm (26%) at Bulgan, between 1993 and 2003. In all areas, peak rainfall occurred in July. Summer and winter temperatures averaged around 15 and −22°C, respectively, at Kherlen Bayan Ulaan, 19 and −14°C at Mandalgobi and 21 and −11°C at Bulgan.

We defined ten ecological sites across the three study areas at different landscape positions in grassland, shrubland or halophytic shrubland vegetation (Table 1). First, denudation planes were identified by drawing summit levels on a 1:200 000 topographical map. We then selected ten typical land units from the sequence of denudation planes (i.e. a land catena): in Kherlen Bayan Ulaan, hill (KH), pediment (KP) and depression (KD); in Mandalgobi, hill (MH), tableland (MT), pediment (MP) and depression (MD); and in Bulgan, upper pediment (BUP), lower pediment (BLP) and depression (BD). The sequence of land units on a catena ran from higher to lower topographic positions in this order within each study area. Consequently, the sites were located along the catenary sequence of denudation planes. Although it was not possible to quantify grazing intensity precisely because of the lack of historical and contemporary records, our previous work suggested that the variation in the relative grazing intensities along the grazing gradient may differ with the actual number of livestock at each site (Sasaki *et al.*, 2008a). Dung counts (number per m^2) decreased as a function of distance from the source of grazing gradient at each site (Table 2). In selecting these sites, we aimed to cover a range of the climatic, geomorphic, edaphic and vegetational variations found within Mongolian rangeland ecosystems.

Table 1 Characteristics of each ecological site in Mongolia, the characteristic shifts in community composition and reliable ecological threshold (RET) along the grazing gradient at each site, and the reference distance along each gradient from a livestock camp or source of water.

Study area, site code	Landscape position	Location	Vegetation type	Dominant plant species and their 'palatability' to sheep and goats*	Characteristic shifts in community composition	RET (m)†	Reference distance (m)‡
Kherlen Bayan Ulaan							
KH	Hill	47°09′N, 109°17′E	Grassland	Grasses (including sedges): *Stipa krylovii* (p), *Agropyron cristatum* (p), *Carex duriuscula* (p)	Nonlinear replacement between perennial grasses or forbs and weedy annual forbs	200	500
KP	Pediment	47°14′N, 108°50′E	Grassland	Grasses: *S. krylovii* (p), *Cleistogenes squarrosa* (p), *C. duriuscula* (p); forbs: *Convolvulus ammanii* (p)	Nonlinear replacement between perennial grasses or forbs and weedy annual forbs	100	1000
KD	Depression	47°04′N, 108°46′E	Grassland	Grasses: *Achnatherum splendens* (p), *S. krylovii* (p), *C. squarrosa* (p)	Nonlinear replacement between perennial grasses or forbs and weedy annual forbs	100	500
Mandalgobi							
MH	Hill	45°47′N, 106°11′E	Shrubland	Shrubs: *Caragana microphylla* (p); forbs: *Artemisia adamsii* (up)	Nonlinear decrease in the cover of shrubs	500	2000
MT	Tableland	45°41′N, 106°27′E	Grassland	Forbs: *Allium polyrrhizum* (p), *Allium anisopodium* (p), *Arenaria capillaris* (up)	Nonlinear replacement between perennial grasses or forbs and weedy annual forbs	200	1000
MP	Pediment	45°41′N, 106°10′E	Grassland	Forbs: *A. polyrrhizum* (p), *Allium mongolicum* (p), *A. anisopodium* (p)	Nonlinear replacement between perennial grasses or forbs and weedy annual forbs	100	1000
MD	Depression	45°38′N, 106°16′E	Halophytic shrubland	Shrubs: *Reaumuria soongorica* (p), *Salsola passerina* (p); forbs: *A. polyrrhizum* (p)	Nonlinear decrease in the cover of shrubs	100	1000
Bulgan							
BUP	Upper pediment	43°54′N, 103°30′E	Grassland	Grasses: *Stipa gobica* (p); forbs: *Artemisia pectinata* (up), *A. polyrrhizum* (p)	Nonlinear replacement between perennial grasses or forbs and weedy annual forbs	1000	2000

Table 1 (Continued)

Study area, site code	Landscape position	Location	Vegetation type	Dominant plant species and their 'palatability' to sheep and goats*	Characteristic shifts in community composition	RET (m)†	Reference distance (m)‡
BLP	Lower pediment	44°14′N, 103°38′E	Shrubland	Shrubs: *Caragana korshinskii* (p), *Brachanthemum gobicum* (up); grasses: *S. gobica* (p)	Nonlinear decrease in the cover of shrubs	500	1000
BD	Depression	44°18′N, 103°35′E	Halophytic shrubland	Shrubs: *Zygophyllum xanthoxylon* (up), *Haloxylon ammodendron* (p), *Kalidium foliatum* (up)	Nonlinear decrease in the cover of shrubs	100	1000

*The information on 'palatability' of dominant species to sheep and goats (p, palatable; up, unpalatable) was provided by Jigjidsuren and Johnson (2003).

†We contrasted the significant responses of forage quality values to the grazing gradient with reliable ecological thresholds (RETs; Sasaki *et al.*, 2011) defined on the basis of the positions of the ecological threshold across three consecutive observation years (2006–2008) to examine the consequences of threshold changes in vegetation for forage quality in communities (for a detailed descriptions of the detection of RETs, see Materials and methods).

‡The reference distance at each ecological site represents the point at which livestock impacts were minimal and was located beyond the normal grazing range of the livestock that were using the camp or source of water.

Plant material sampling

In this study, we used a grazing gradient approach (Andrew, 1988). We used the distance (in metres) from a camp or source of water (hereafter, the 'gradient source') to represent relative grazing intensity, according to previous studies where this approach was applied (Landsberg *et al.*, 2003; Todd, 2006; Sasaki *et al.*, 2008a). In our previous work (Sasaki *et al.*, 2008a, 2011), we defined a 'reference distance' (Table 1), which represented the point at which livestock impacts were minimal, chosen outside the normal grazing range of the livestock from the gradient source.

Available forage in arid and semi-arid rangelands, which is the available parts of plants used by ruminants (Vallentine, 1990), is defined as the whole aerial parts of herbaceous plants and annual new shoots of shrubs likely to be grazed by sheep and goats (Thalen, 1979). The whole aerial parts of herbaceous plants, including edible stems and annual new shoots of shrubs, have been termed as 'herbage', and their nutritional value as 'herbage nutritive value' (Allen *et al.,* 2011). In this study, we have used this terminology. Between June and August 2008, at each site, we sampled all above-ground standing plant material (excluding woody parts of shrubs) within three 50 cm × 50 cm quadrats along a transect placed at set distances along the grazing gradients (three gradient replicates radiating in different directions from the gradient source). In general, we sampled transects at 10, 50, 100, 200, 500 and 1000 m from the gradient source. At KH and KD, because of the difference in topography over 600 m from the gradient source, we decided to sample plant materials up to 500 m in order to minimize confounding effects of topographical differences on the results. We additionally sampled at 1500 and 2000 m at KH and BUP, because plants damaged by grazing and various amounts of dung were still found at 1000 m from the gradient source. Each 50 cm × 50 cm quadrat on a transect was laid out at intervals of 5 m for the quadrats located 10–50 m from the source and at the intervals of 10 m thereafter.

The plant samples from each quadrat were dried to constant mass and then weighed. The samples were then ground in a mill to form one composite sample per transect. This procedure was intended to minimize the potential effects of selective feeding by livestock at different sampling locations on the variations in the nutritive value and yield. The samples were analysed in the laboratory for the concentration of crude protein (CP), neutral detergent–insoluble crude protein (NDICP), acid detergent–insoluble crude protein and fatty acids (FA) according to the methods described by AOAC (2000). The concentration of neutral detergent fibre (NDF), acid detergent fibre, acid detergent lignin

Table 2 Changes in dung counts (mean ± SD) along the grazing gradient at each ecological site. Dung counts decreased as a function of distance from the gradient source.

Study area, site code	Distance from the source of grazing gradient (m)							
	10	50	100	200	500	1000	1500	2000
Kherlen Bayan Ulaan								
KH	610·7 ± 195·9	218·0 ± 138·6	31·6 ± 46·1	10·7 ± 7·3	7·6 ± 3·6	–	–	–
KP	627·2 ± 548·8	41·1 ± 23·8	38·3 ± 13·0	16·4 ± 3·9	8·3 ± 3·6	4·1 ± 4·0	–	–
KD	400·5 ± 446·9	231·8 ± 197·2	33·5 ± 10·6	9·9 ± 3·2	8·2 ± 1·2	–	–	–
Mandalgobi								
MH	84·4 ± 17·8	55·0 ± 18·8	31·3 ± 13·0	20·8 ± 5·9	14·2 ± 4·4	11·1 ± 6·9	12·3 ± 5·1	8·0 ± 2·2
MT	288·1 ± 131·6	81·1 ± 67·7	24·2 ± 18·5	4·6 ± 2·3	2·7 ± 0·7	2·8 ± 1·1	–	–
MP	519·8 ± 250·2	25·9 ± 13·5	19·4 ± 8·7	15·3 ± 5·3	6·7 ± 6·5	6·5 ± 1·3	–	–
MD	533·87 ± 393·9	37·2 ± 23·4	22·6 ± 7·3	8·2 ± 3·1	4·7 ± 3·0	5·6 ± 2·3	–	–
Bulgan								
BUP	45·2 ± 17·5	36·0 ± 7·8	20·1 ± 2·2	31·0 ± 4·6	10·1 ± 3·4	4·0 ± 2·1	2·8 ± 0·8	3·2 ± 1·3
BLP	13·5 ± 7·8	15·5 ± 7·2	6·3 ± 3·3	2·5 ± 1·6	4·7 ± 1·3	2·4 ± 1·6	–	–
BD	104·5 ± 136·3	12·4 ± 12·7	2·0 ± 1·3	0·9 ± 0·6	1·1 ± 1·2	1·3 ± 1·5	–	–

and ash was determined according to the method described by Van Soest (1994). Non-fibre carbohydrates (NFC) were calculated as (NFC = 100 − CP − [NDF − NDICP] − FA − Ash). The total digestible nutrients (TDN) were calculated using the equation proposed by NRC (2001): (TDN = dNFC + dCP + 2·25 × dFA + dNDF − 7), where dNFC, dCP, dFA and dNDF represented each of the digestible nutrient components. The metabolizable energy (ME; MJ kg^{-1}) was calculated as (ME = TDN × 0·82 × 0·04409 × 4·182).

Ecological threshold along a grazing gradient

Our previous work (Sasaki *et al.*, 2011) revealed the reliable ecological threshold (RET; Table 1) at each site defined on the basis of the positions of the ecological threshold across three consecutive observation years (from 2006 to 2008: note that sampling of plant material for the analyses of nutritive value and yield of herbage was conducted once in 2008). To determine the ecological threshold within each observation year, Sasaki *et al.* (2011) used piecewise regression models (*sensu* Toms and Lesperance, 2003) fitted to relationships between the floristic composition data (i.e. the scores on the first axis of detrended correspondence analysis, DCA; Legendre and Legendre, 1998) for each sample transect and the distance of each transect from the source of grazing gradient across observation years at each site. The form of piecewise regression model is (Score of DCA axis 1 = $a + b \times$ Distance, if Distance $\leq D$; Score of DCA axis 1 = $a + b \times$ Distance + $c \times$ [Distance − D], if Distance > D), where a, b and c are the model parameters, and D is the breakpoint representing ecological threshold. The definitive distance corresponding to the ecological threshold at each site was thus identified for the data within each observation year to set a 'RET' based on each calculated breakpoint. The RET was set as the nearest sampling distance located outside all the positions of ecological threshold across observation years at each site.

The threshold responses of vegetation to grazing reflect rapid and nonlinear replacement of or decrease in plant cover at each site (Table 1; Sasaki *et al.*, 2008a, 2011): rapid and nonlinear replacement between perennial grasses or forbs and weedy annual forbs at KH, KP, KD, MT, MP and BUP (grassland sites); and a rapid and nonlinear decrease in the shrub cover at MH, MD, BLP and BD (shrubland sites). Differences in the vegetation type at each site (Table 1) resulted in differences among sites in the responses of functional groups to grazing (Sasaki *et al.*, 2008a, 2011).

In the following analyses, we examined the changes in the nutritive value and yield of herbage along a grazing gradient at grassland and shrubland sites (the data from KH, KP, KD, MT, MP and BUP, and the data from MH, MD, BLP and BD were pooled, respectively). We then discussed whether these changes along a grazing gradient reflect differential responses of vegetation to grazing between grassland and shrubland sites.

Data analyses

To determine the changes in the nutritive value and yield of herbage along the grazing gradient at each site with no prior assumption about a given response's exact form and shape, we used a cubic smooth spline within the framework of generalized additive mixed models (Hastie and Tibshirani, 1990): [$H = s(x)$], where H is the

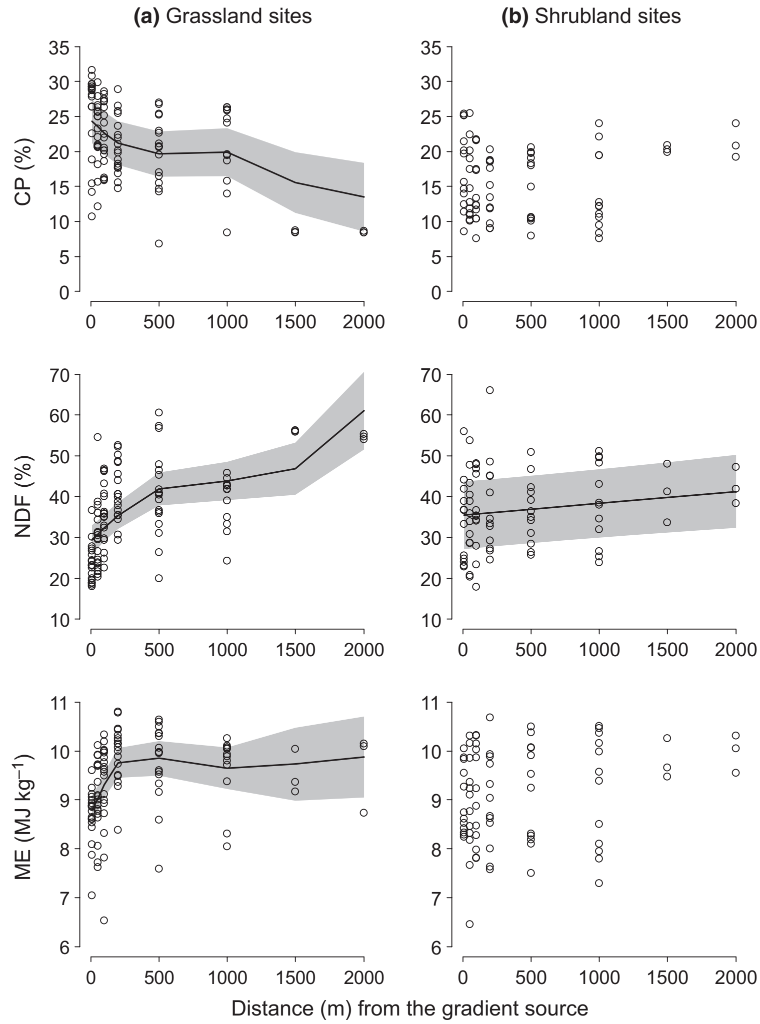

Figure 1 Trends in the herbage nutritive value (CP, crude protein; NDF, neutral detergent fibre; ME, metabolizable energy) plotted against distance from the gradient source: (a) at the grassland sites (the data from KH, KP, KD, MT, MP and BUP were pooled), (b) at the shrubland sites (the data from MH, MD, BLP and BD were pooled). Black solid lines indicate significant trends (approximate $P < 0{\cdot}05$). The grey zones indicate the 95% confidence interval.

herbage nutritive value (CP, NDF and ME concentrations), herbage yield or herbage nutritive yield (CP and ME yields) for each transect placed at set distances (generally, 10, 50, 100, 200, 500 and 1000 m from the gradient source; see the Plant material sampling subsection of Materials and methods) along the grazing gradients (three gradient replicates), and $s(x)$ is a function of the predictor variable (here, distance from the gradient source), which is defined locally by a cubic smooth spline function. The degree of smoothing for the predictor was determined by general cross-validation (Wood, 2006). In these models, we have accounted for the effect of potential difference in livestock number and composition, landscape positions and climatic conditions between sites on the model prediction by adding the site identity as a random effect. Constraints on the data from our sampling design (i.e. the potential correlation between sample transects) were controlled by adding the gradient identity as a random effect. All statistical analyses were performed with the R software v. 2.7.0 (R Development Core Team, 2008).

Results

Changes in the herbage nutritive value (CP, NDF and ME concentrations) along a grazing gradient at the grassland sites (the data from KH, KP, KD, MT, MP and BUP were pooled for the analyses) were all significant (Figure 1a; $P < 0{\cdot}05$). Herbage CP concentration increased in the direction of the gradient source, and it increased sharply in approaching the gradient source. NDF concentration decreased in the direction of the gradient source and decreased sharply in approaching the gradient source. ME concentration was relatively constant below a certain level of grazing intensity and then exhibited a sharp decrease in approaching the

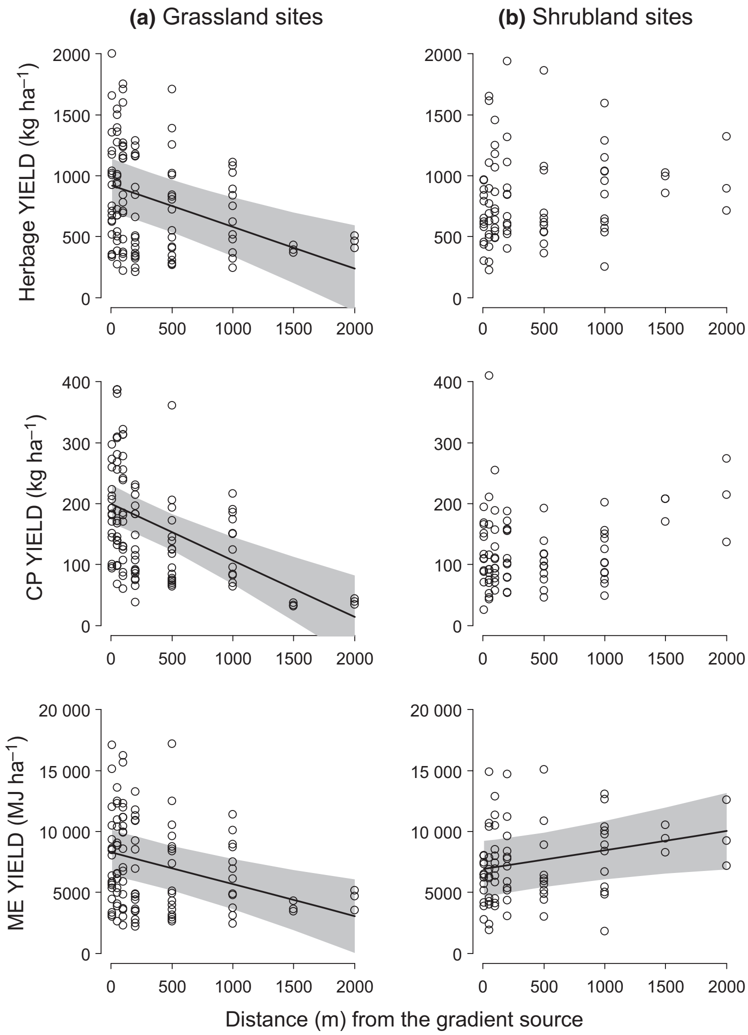

Figure 2 Trends in the herbage yield (Herbage YIELD) and herbage nutritive yield (CP YIELD, crude protein yield; ME YIELD, metabolizable energy yield) plotted against distance from the gradient source: (a) at the grassland sites (the data from KH, KP, KD, MT, MP and BUP were pooled), (b) at the shrubland sites (the data from MH, MD, BLP and BD were pooled). Black solid lines indicate significant trends (approximate $P < 0{\cdot}05$). The grey zones indicate the 95% confidence interval.

gradient source. Rapid changes in these herbage nutritive values can be attributed to the existence of RET (Table 1), which generally occurred at 100–200 m from the gradient source at the grassland sites. Herbage yield, CP and ME yields gradually increased in the direction of gradient source ($P < 0{\cdot}05$; Figure 2a).

At the shrubland sites (the data from MH, MD, BLP and BD were pooled for the analyses), CP and ME concentrations did not change significantly along a grazing gradient (Figure 1b). NDF concentration gradually decreased in the direction of gradient source ($P < 0{\cdot}05$; Figure 1b). Changes in the herbage nutritive value were not associated with the existence of RET (Table 1). Herbage yield and CP yield did not change significantly along a grazing gradient (but herbage yield tended to decrease; $P = 0{\cdot}09$), whereas ME yield gradually decreased in the direction of gradient source ($P < 0{\cdot}05$; Figure 2b).

Discussion

Changes in the nutritive value of herbage (CP, NDF and ME concentrations) along the grazing gradient at the grassland sites (Figure 1a; the data from KH, KP, KD, MT, MP and BUP were pooled) were probably attributed to nonlinear rapid replacement between perennial grasses or forbs and weedy annual forbs (Table 1; Sasaki *et al.*, 2008a, 2011).These general relationships between the herbage nutritive value and livestock grazing can be detected even though livestock number and composition, landscape positions and climatic conditions differed between the sites. With increased grazing intensity as the distance from a camp or source of water decreased, soil organic carbon and total nitrogen both increase (Sasaki *et al.*, 2008b) owing to the redistribution of nutrients through urine and dung. Species associated with resource-rich patches tend to be fast-growing, morphologically plastic plants with short-lived, nutrient-rich leaves (Diaz and Cabido, 1997; Grime *et al.*, 1997). In contrast, plants common to nutrient-limited environments are often characterized by inherently slow growth, fibrous long-lived leaves and high investment in support and storage organs (Diaz and Cabido, 1997; Grime *et al.*, 1997). CP concentration increased sharply, whereas NDF concentration decreased sharply in approaching the source of grazing gradient, generally supporting these predictions. The increase in CP concentration and decrease in NDF concentration might result not only from changes in community composition but also from the maintenance of green and leafy herbage under some moderate level of herbivory (De Santis *et al.*, 2004; Henkin *et al.*, 2011). As the herbage nutritive value depends on the ratio of positive (e.g. protein, fat, carbohydrates) to neutral or negative (e.g. fibre, lignin) nutrients, we cannot assess the herbage nutritive value by using only a single parameter; in our study, the increase in CP and decrease in NDF along the grazing gradient do not necessarily indicate the improvement of herbage nutritive value by grazing, because ME concentration decreased sharply in approaching the gradient source. The ME is calculated as the sum of digestible NFC, CP, FA and NDF (NRC, 2001). Therefore, ME can be utilized as a main index of herbage nutritive value and is considered one of the most important properties in determining animal production (NRC, 2001). Herbage along a grazing gradient at the sites covered the nutrient requirements for sheep and goats in terms of the nutritive value [feed concentration requirements for the maintenance of a 60-kg sheep and a 60-kg goat are 95 and 96 g CP kg^{-1}, and 8·36 and 8·40 MJ kg^{-1} of ME, respectively; (NRC, 1981, 1985)]. Nonetheless, the dramatic decrease in ME concentration suggested a marked reduction in the herbage nutritive value with severe grazing. Furthermore, because weedy annual forbs are much less palatable than perennial grasses and forbs in the study areas (Jigjidsuren and Johnson, 2003), communities that shift to dominance by weedy annual forbs are of little forage value. These arguments presented here also suggest that gradual increases in the yields of CP and ME in the direction of the gradient source (Figure 2a) at the grassland sites did not necessarily indicate an improvement of the rangeland condition. Thus, the assessment of rangeland condition should be based on the changes in the herbage nutritive value as well as yield associated with changing community composition along a grazing gradient at the local scale.

In contrast, at the shrubland sites, we could not detect any significant trends in the herbage nutritive value along the grazing gradient (Figure 1b; except for NDF concentration that showed, significantly, a slightly decreasing trend). Trends in the herbage yield and the ME yield were decreasing (but the trend in herbage yield was not significant) in the direction of the gradient source (Figure 2b). This result suggested that a nonlinear decrease in the cover of shrubs (Table 1) would be reflected in changes in the herbage quantity rather than quality. In addition, Sasaki *et al.* (2008b) suggested that the magnitudes of changes in community composition at the shrubland sites were relatively small compared to those at the grassland sites. Land managers should be aware that impacts of severe grazing at shrubland sites would lead to a decrease in the herbage quantity even if quality is not affected.

Conclusions

Our study showed that the nutritive value and yield of herbage can be modified greatly in association with threshold responses of community composition to livestock grazing. In our previous work (Sasaki *et al.*, 2008a, 2011), we demonstrated that an ecological threshold corresponding to abrupt changes in ecological responses will more readily translate into management guidelines. Optimizing rangeland use, such that the levels of grazing do not exceed the ecological threshold, through utilizing ecological indicators (e.g. the cover of certain plant functional groups) which can forewarn its occurrence (Sasaki *et al.*, 2011), would prevent land degradation and the consequent loss of ecosystem services. In particular, the drastic loss of the herbage nutritive value in association with threshold responses of vegetation to grazing at the grassland sites has important implications for rangeland management, because extensive areas supporting grassland vegetation are probably of greater value for providing substantial amounts of forage resources required by a region's livestock.

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