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TOWARDS PARTICIPATORY CONSERVATION IN THE TRANS-HIMALAYA: CONSERVING RANGELANDS

FOR WILDLIFE AND PEOPLE'S LIVELIHOODS

Grantee:

SUMANTA BAGCHI
Nature Conservation Foundation
3076/5, IV-Cross, Gokulam Park, Mysore, Karnataka – 570002, India.
Tel: +91 821 2515601, Fax: +91 821 2513822, E-Mail: sumanta (*at*) ncf-india (*dot*) org

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SUMMARY

This interim progress report summarizes data collected under the research project titled 'TOWARDS PARTICIPATORY CONSERVATION IN THE TRANS-HIMALAYA: CONSERVING RANGELANDS FOR WILDLIFE AND PEOPLE'S LIVELIHOODS' in Kibber Wildlife Sanctuary (32° N, 78° E) in Spiti region of northern India between May and August 2006. During this period, 8 new herbivore exclosures were setup alongside the 16 that were setup in 2005. Major emphasis during this field season was on estimating impacts of grazing (by livestock and wild herbivores) on plant productivity, nutrient cycling and soil water retention. Results from laboratory analysis of samples for assessing nutrient cycling will be available by March-April 2007, and are not part of this report. These will be made available with the next interim report.

Chapter 1 summarizes the results from an herbivore exclusion experiment with fences set up in 2005, over plant production, plant species turnover, and soil moisture retention. Results show that grazing: (1) stimulates production, (2) reduces soil moisture as the growth season progresses (May to August), (3) reduces litter quantity and, (4) reduces belowground plant allocation. These indicate that grazing can also influence soil biogeochemistry and future work will address this aspect.

Chapter 2 summarizes results from a more detailed study on soil moisture retention. Results show that a positive-feedback mediated resource concentration mechanism allows plants growing on slopes to be more efficient in harvesting rain water compared to plants growing flat terrain. This corresponds to higher relative allocation to belowground biomass for plants on slopes, and hence, makes them more susceptible to grazing pressures. The implications for sustainable management of these rangelands are discussed.

Future work (2006 – 2007) will address differences in responses at the plant-soil interface to grazing by native and exotic herbivores, combining samples from pre-existing (2005), and newly established (2006) fences.

SUMMARY OF EXPENDITURE 2005-06

HEAD	EXPENDITURE FROM	
	TOTAL EXPENDITURE (INR)	RUFFORD SMALL GRANT (INR)
Vehicle hire, travel and freight	41,474	10,524
Field equipment	112,088	11,932
Salaries of field assistants	48,000	16,850
Communication	686	0
Field and Lab consumables	38,809	36,006
Rent and Accommodation	18,854	0
<i>Per diem</i>	75,000	45,000
Total	32,2411	120,312
	≈ GB £ 4,134*	≈ GB £ 1,543*

*1 GB £ = 78 INR

GRAZER EFFECTS ON PLANT COMMUNITIES, PRODUCTION, AND SOIL MOISTURE IN THE HIGH-ALTITUDE TRANS-HIMALAYAS, NORTHERN INDIA

SUMANTA BAGCHI,^{1,2†} AND MARK E. RITCHIE¹

¹*Biological Research Labs, Syracuse University, 130 College Place, Syracuse, NY – 13244, USA.*

²*Nature Conservation Foundation, 3076/5, IV-Cross, Gokulam Park, Mysore, Karnataka – 570002, India.*

Abstract. Grazer effects on plant production, plant species turnover, and soil moisture retention are measured using replicate herbivore exclosures in Trans-Himalayan rangelands of Kibber Wildlife Sanctuary, northern India. Annual net primary production was 33.8 (\pm 3.7 SE) g m⁻²; and was stimulated by 84.8% (\pm 14.2% SE) through grazing that amounts to consumption of 47.0% (\pm 5.0% SE) of plant production during the growth season (May-August). Grazing also reduced soil moisture as the growth season progressed and also negatively affected plant allocation to belowground biomass as a fraction of total plant biomass. Herbivore exclusion for 2 growth seasons did not bring about plant community changes. These results suggest that grazing exercises strong top-down control over ecosystem processes in the Trans-Himalayas and can also influence biogeochemical functions. This aspect will be investigated in future work.

Keywords: ecosystem function, grazing, herbivory, plant community, production, sustainability

INTRODUCTION

Grazing ecosystems are unique in their ability to sustain productivity despite intense and chronic levels of herbivory (Frank et al. 1998). A long coevolutionary history between plants and herbivores since the Miocene (Stebbins 1981), has led to many co-adaptations such as compensatory growth by plants and modulation of nutrient cycling by herbivores (Hobbs 1996). Native large grazing mammals were characteristic of nearly one-half of the earth's terrestrial realm until 150 years ago (McNaughton 1985) but, today they are progressively being replaced by livestock (Prins 1992).

Given the nature of this interaction, herbivores can exercise strong control over ecosystem functioning by influencing plant production, nutrient cycling and soil water distribution (Dyer et al. 1993, Chapin et al. 1997), that are conventionally studied using herbivore exclusion experiments (Milchunas and Lauenroth 1993). These have shown that herbivore effects on ecosystem functions can be nearly opposite (positive or negative, Milchunas and Lauenroth 1993, Hobbs 1996). Chase et al. (2000) suggest that these nearly opposite effects can be explained by incorporating compositional turnover of plants following herbivore exclusion. In general, moderate grazing can stimulate plant production via compensatory growth (McNaughton 1976); and on infertile soils, grazing can decelerate nutrient cycling (Ritchie et al. 1998). Also at low levels of precipitation, herbivory has a high impact on plant biomass, but low impact on plant species turnover (Chase et al. 2000). In comparison, the effects on soil water availability and distribution remain poorly understood (Rietkerk et al. 1997), despite most grazing ecosystems occurring in semiarid to arid conditions. Here, we provide data from a field experiment on grazer effects on plant production, plant species turnover, and soil water retention from the nutrient-poor and water-limited Trans-Himalayan grazing ecosystem in northern India. Given the low levels of soil N and precipitation in the Trans-Himalaya, we expected herbivore exclusion to (1) increase standing plant biomass, (2) but the effect on plant production (positive or negative), would depend on grazing intensity (high or low) (3) if plants show compensatory growth, this would enhance water requirements and reduce soil moisture levels, and (4) have weak effect on plant species composition.

[†] Correspondence: Nature Conservation Foundation, 3076/5, IV-Cross, Gokulam Park, Mysore, Karnataka – 570002, India. Tel: +91 821 2515601, Fax: +91 821 2513822, E-Mail: sumanta (at) ncf-india (dot) org

METHODS

Using replicate herbivore exclosures in different rangelands of Kibber Wildlife Sanctuary (32° N, 78° E), northern India; we measured grazer impacts on plant production, plant species turnover, and soil moisture retention. These rangelands are part of the vast Trans-Himalayan grazing ecosystem with elevation between 4300 and 4500 m, and annual precipitation of 200 mm. These are grazed by wild herbivores (bharal, *Pseudois nayaur*; and ibex *Capra sibirica*) alongside various livestock (yak, cattle, yak-cattle hybrids, donkey, goat and sheep). Following Himalayan orogeny, this Tibetan ecosystem attained its present average elevation (3500 – 4000 m) by the Miocene (8 million years ago), and became progressively arid through the Pleistocene (Harrison et al. 1992). The vegetation is dry alpine steppe formed by grasses, sedges and shrubs adapted to a cold-arid environment while the tree layer is absent. Climate is cold and arid with temperatures dropping below –30° C between November and March, allowing a short growth season for plants (May-August, Bagchi et al. 2006).

Fences (10 X 10 m, $n = 15$) were set up at the beginning of the growth season 2005 and data were collected through the growth season of 2006. During this 2 year period, the region received 78 mm of rain and 178 cm of snow. By August 2006, the fences had excluded grazing in the study plots by large mammals for 2 growth seasons. Each fenced plot was paired with a similar, adjacent, unfenced control plot to provide two treatment levels – grazed and ungrazed.

Annual net primary productivity (ANPP) was measured in the control plots using movable cages (1 X 1 m, $n = 2$ quadrats in each plot) at monthly intervals (McNaughton et al. 1996). All live aboveground tissue was clipped to ground level from the quadrats. Collected live biomass was subsequently separated into 3 categories – grasses, sedges and shrubs. At the end of the growth season, biomass was clipped from similar quadrats in the fenced plots. Grazing intensity was measured from the difference in standing biomass of fenced and control plots (McNaughton 1979). At the end of the growth season (August 2006), all litter including standing dead biomass was also collected separately from each quadrat in fenced and control plots. Standing belowground biomass was collected using a 2.5 cm radius and 20 cm deep, soil core from the center of each quadrat. Subsequently, the soil cores were washed in running water using 1 mm sieves to separate all belowground plant tissues (including roots, rhizomes and scaly layers) from adhering soil. All samples were oven dried to obtain dry weights.

Soil moisture was measured as Volumetric Water Content (VWC as %) at 4 – 6 random locations in each fenced and control plot at monthly intervals between May and August 2006, using a 20 cm long, time domain reflectometry probe (TDR, Spectrum Technologies Inc., Plainfield, USA). All data from fenced and control plots were compared using General Linear Models (GLMs) in SAS v. 9.1 (SAS Institute, Cary, USA) at $\alpha = 0.05$.

Relative abundance and community structure was estimated as percentage cover of different species using the line intercept method (Muller-Dumbois and Ellenberg 1974), with 50 points at every 0.5 m along a 25 m. These data were collected once at the beginning of the growth season in 2005 and again at the end of the growth season in 2006, to assess vegetation community shifts due to herbivore exclusion. Changes in species composition were analyzed using Bray-Curtis similarity index (Bray and Curtis 1957), between the grazed and paired control plot after 2 years of herbivore exclusion, relative to the similarity present before herbivores were excluded. Bray-Curtis similarity

index was calculated as $S_{jk} = 100 \left(1 - \frac{\sum_{i=1}^p |y_{ij} - y_{ik}|}{\sum_{i=1}^p |y_{ij} + y_{ik}|} \right)$, where S_{jk} is the similarity between sites j and k ,

y_{ij} is the cover of i^{th} species in the j^{th} sample, and y_{ik} is the cover of i^{th} species in the k^{th} sample,

summed across all p species (Magurran 1988). Statistical significance of plant community change was assessed with Analysis of Similarity (ANOSIM) following Clarke and Warwick (1994) using 5000 randomized iterations in PRIMER 5 (Plymouth Routines in Multivariate Ecological Research, Clarke and Gorley 2001). ANOSIM evaluates similarities between groups, analogous to ANOVA, while testing for statistical significance via Monte Carlo permutations (Clarke and Warwick 1994).

RESULTS

Standing biomass and grazing intensity

Grazing significantly reduced standing live biomass (Fig. 1; $F_{1,28} = 6.06$, $P = 0.02$). Grazing intensity was high, as herbivores removed 47.0% ($\pm 5.0\%$ SE) of plant production during the growth season. Grazing intensity was unrelated to site productivity ($P = 0.36$). Grazing significantly reduced litter quantity (Fig. 1; $F_{1,28} = 5.93$, $P = 0.02$). We did not find grazer effects on belowground standing biomass (Fig. 1; $F_{1,28} = 1.01$, $P = 0.33$). However, grazing reduced plant allocation to belowground biomass as a fraction of total plant biomass, i.e. $\text{Biomass}_{\text{below}} / (\text{Biomass}_{\text{above}} + \text{Biomass}_{\text{below}})$, from 35.1% ($\pm 5.1\%$ SE) in ungrazed plots to 20.6 ($\pm 2.7\%$ SE) in grazed plots ($F_{1,28} = 4.62$, $P = 0.04$, log-transformed to achieve homogeneity of variance).

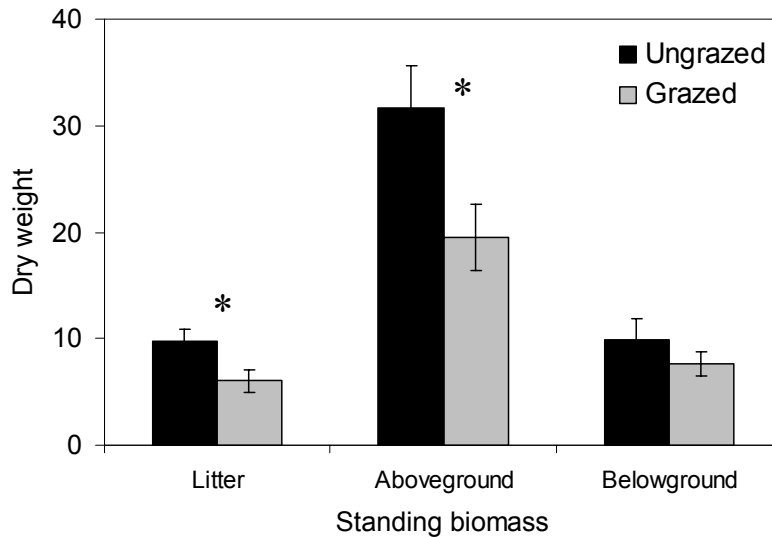


FIG 1. Standing biomass (g m^{-2}) of litter, above and belowground plant tissue in grazed and ungrazed plots in Trans-Himalayan rangelands, northern India. Asterisks denote a significant difference ($P < 0.05$) between the grazed and ungrazed plots.

ANPP: grazer stimulation and grazing intensity

Grazing facilitated production of these rangelands (Fig. 2). Aboveground production varied considerably across sites and was $33.8 (\pm 3.7 \text{ SE}) \text{ g m}^{-2}$ in ungrazed plots, and $58.7 (\pm 5.8 \text{ SE}) \text{ g m}^{-2}$ in grazed plots, such that grazer stimulation of aboveground production was 84.8% ($\pm 14.2\%$ SE). We examined the influence of two factors – herbivory and local site conditions, on the observed variability in grazer effects. Local site conditions were taken as the ungrazed plant production, and herbivory was taken as intensity of grazing (percentage of biomass removed at a site). Observed variation in grazer stimulation among sites was unrelated to herbivory (grazing intensity, Fig 3a), but, was related to local site conditions (Fig. 3b; $R^2 = 0.33$, $P = 0.02$). Less productive sites showed greater compensatory growth than more productive ones.

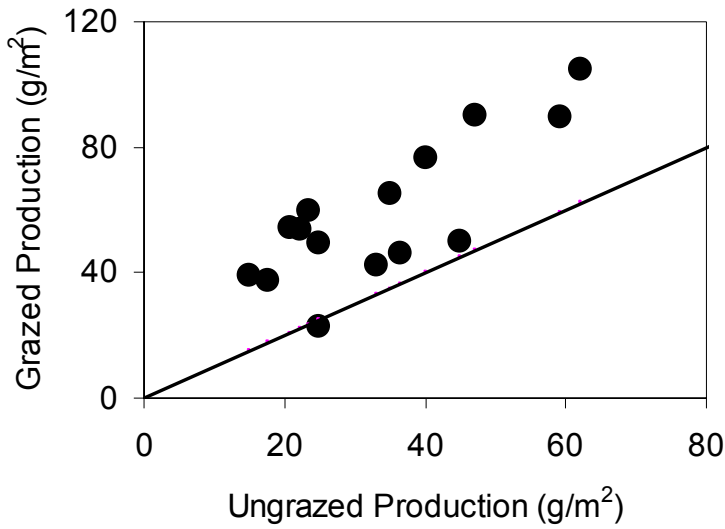


FIG 2. Relation between grazed and ungrazed annual net aboveground production in Trans-Himalayan rangelands, northern India. The diagonal line represents equality, and grazed production is seen to be greater than ungrazed production at most sites.

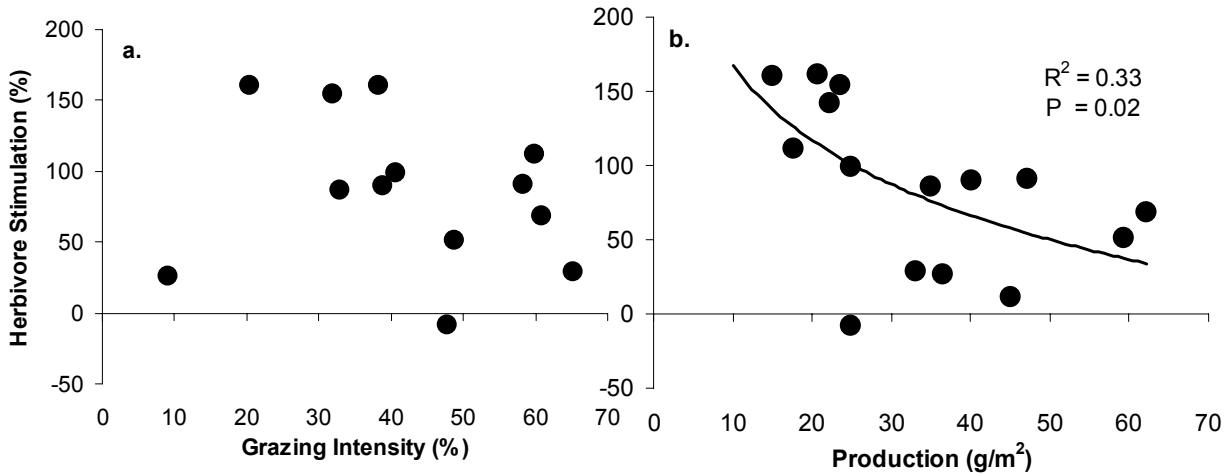


FIG. 3. Relationships between herbivore stimulation of plant production, as percent increase in production relative to ungrazed production at a site, with grazing intensity as percentage of total production consumed by herbivores (a); and with ungrazed local site production (b). Herbivore stimulation is not strongly related to grazing intensity, but shows a declining trend with local site production.

Growth patterns over time

Overall production (grazed plots) increased monotonically as the growth season progressed (Fig. 4). However, patterns of growth were dissimilar among the 3 functional types. Growth in grasses and forbs tapered off after July, even though most of the rainfall was received in mid-July. But, sedges continued to grow till August, after which senescence set in. Lack of growth in grasses and forbs after rains is possibly due to them being in inflorescence by July, and not investing in aboveground tissues after flowering.

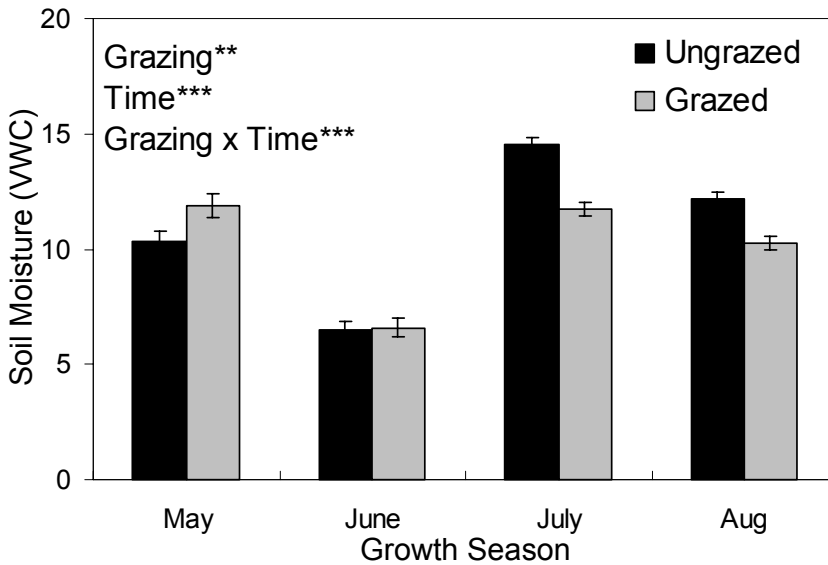


FIG. 4. Changes in soil moisture (Volumetric Water Content as %) over the growth season in grazed and ungrazed plots in Trans-Himalayan rangelands, northern India. Grazing is seen to deplete soil moisture as the growth season progresses.

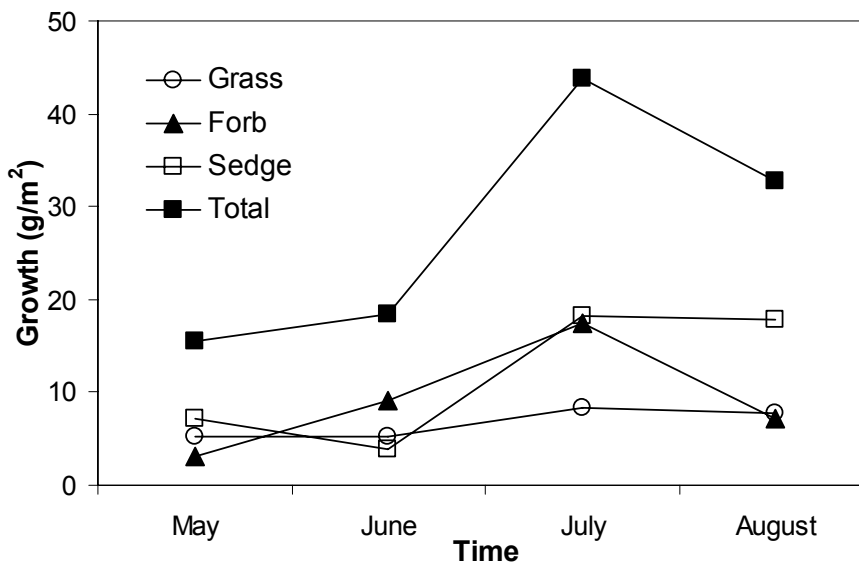


FIG. 5. Temporal patterns of mean production in grazed plots in Trans-Himalayan rangelands, northern India. Growth in grasses and forbs is seen to taper off after July, whereas, sedges continued to grow till August.

Plant community change

Results from ANOSIM suggest that herbivore exclusion for 2 growth seasons did not bring about changes in plant species composition. Similarity (or conversely dissimilarity) in plant species composition between paired grazed and ungrazed plots did not change over the period of exclusion ($P = 0.78$), and there were no directional community shifts.

Soil moisture over time

Grazing reduced soil moisture as the growth season progressed (Fig. 4), and there was a significant Grazing X Time interaction in repeated-measures ANOVA ($F_{3,42} = 9.83$, $P < 0.001$).

DISCUSSION

Grazing intensity in these rangelands is comparable to the global average, even though ANPP is about 2 SD below the global average for grasslands (Milchunas and Lauenroth 1993). Since grazer stimulation was greater at low-productive sites, this implies defoliation and consequent canopy thinning does not favor regrowth when vegetation is dense. This suggests, plant competition is strong for belowground resources (water) and weak for light. In more productive ecosystems (Huisman and Olff 1998, Huisman et al. 1998), plants become light-limited when aboveground biomass approaches 300 g m⁻². Since biomass in these arid rangelands is about a tenth of this threshold, these data suggest belowground plant competition is more important than for light.

Some previous studies have shown that grazers increase root production and, grazer stimulation of belowground production is expected to be greater than stimulation of aboveground production (Frank et al. 2002). Although we did not measure root production, grazing reduced belowground biomass allocation. So, these data suggest high rates of root turnover and translocation to shoots following defoliation, which can be experimentally tested in future work. If herbivore-induced root mortality is indeed found to be a major factor, then, grazing is expected to play a major role in C-enrichment of these soils throughout their development (Frank and Groffman 1998). This would also facilitate microbial activity, and lead to acceleration on N-cycling. Soil samples have been collected to assess C:N ratios alongside resin-bag samples to assess net N-mineralization. These data on grazer impacts on soil chemical processes will be available by April 2007 and will be made available with the next interim report.

Overall, herbivores are seen to exercise strong top-down effects on ecosystem functions in the Trans-Himalaya and future work will facilitate the development and implementation of appropriate grazing policies towards long-term sustainable production (and use) of this ecosystem.

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LANDSCAPE CONTROL OVER PLANT-SOIL POSITIVE FEEDBACKS IN THE ARID TRANS-HIMALAYAN GRAZING ECOSYSTEM

SUMANTA BAGCHI,^{1,2,†} CHARUDUTT MISHRA,² AND MARK E. RITCHIE¹¹*Biological Research Labs, Syracuse University, 130 College Place, Syracuse, NY – 13244, USA.*²*Nature Conservation Foundation, 3076/5, IV-Cross, Gokulam Park, Mysore, Karnataka – 570002, India.*

Abstract. Self-organized patchiness in vegetation is seen in many water-limited grazing ecosystems, including the cold-arid high-altitude Trans-Himalayas. But, here patterns are more prominent on slopes compared to flat areas. Background theory is reviewed which leads to the hypothesis that sloping areas exhibit a stronger positive feedback between vegetation and water retention compared to flats. Field data are collected from both landscape categories, to compare water retention in vegetated and adjacent barren patches. Results show that vegetation on slopes retains more soil moisture following rainfall. This was established further through a small scale irrigation experiment. Also, plants invest greater proportion of biomass in belowground tissues when growing on slopes. Thus, landscape is seen to influence plant-soil feedback, and this requires different plant strategies of biomass allocation above and belowground.

Keywords: self organized patchiness, bistability, catastrophic shifts, alternate vegetation states, grazing, herbivory

INTRODUCTION

Self-organized patchiness is seen in the vegetation of many water-limited grazing ecosystems. Patchy distribution of plant biomass leads to clear demarcation between vegetated and barren patches. Frequently, these patches appear as stripes, spots, rosettes, and maze-like labyrinths (Rietkerk et al. 2004). Such self-organized vegetation are susceptible to catastrophic shifts with concomitant changes in ecosystem functions and services and understanding how such 2-phase mosaics respond to environmental change, including human exploitation, is a frontier of ecology with important applications for sustainable management and recovery strategies (Rietkerk et al. 1997). Catastrophic shifts are attributed to existence of two alternative stable states in these ecosystems, determined by two attractors, which invokes the notion of bistability (Rietkerk and van de Koppel 1997). Existing theory explains these patterns as a positive feedback between consumers (plant) biomass and limiting resources (usually water in arid regions). A resource concentration mechanism arises from this feedback leading to an ecosystem state that develops the localized structures visible in nature. Thus, these localized structures or patchiness emerge from interactions at the plant-soil interface through internal mechanisms (Klausmeier 1999). For arid regions, the chief resource concentration mechanism involves improved water retention in soil when vegetation provides root channels (Walker et al. 1981). Higher plant density facilitates water infiltration and vegetation persists once established; but bare soil is too hostile for propagules to colonize. Consequently, if overgrazing reduces plant biomass below a critical threshold, the vegetation shifts to a stably degraded state unless water availability is increased dramatically beyond certain breakpoint values as documented in many arid grazing systems around the world (van de Koppel and Rietkerk 2000).

The Trans-Himalaya in central Asia is a vast cold-arid high-altitude grazing ecosystem (larger than Alaska), with long coevolutionary history between soils, plants and herbivores (Schaller 1998). Following Himalayan orogeny, this Tibetan ecosystem attained its present average elevation (3500 – 4000 m) by the Miocene (8 million years ago), and became progressively arid with open steppe vegetation through the Pleistocene (Harrison et al. 1992). Most of the area is rugged and mountainous, thus leading to high rates of surface runoff, both from snow melt as well as rainfall. And expectedly, vegetation in the Trans-Himalaya exhibits clear patterns of patchiness – interlinked stripes under graminoids and maze-like labyrinths under shrubs (at 1 – 5 m scale). But, these patterns are best established on sloping terrain. In flat areas such as plateau uplands and valley bottoms, vegetated patches do alternate with bare regions and involve the same suite of plant species as on the slopes. However, the pattern does not closely resemble the mazes on slopes, but rather appears as dis-

† Correspondence: Nature Conservation Foundation, 3076/5, IV-Cross, Gokulam Park, Mysore, Karnataka – 570002, India. Tel: +91 821 2515601, Fax: +91 821 2513822, E-Mail: sumanta (at) ncf-india (dot) org

ordered spots or clusters of shrubs and forbs, often in a grass matrix (Fig. 1). In other words, vegetation on slopes appears more ‘connected’ than on flats, whereas on flats it is a rather uniform scatter of plants. We hypothesize that the difference in patterns between slopes and flats could be a result of the strength of the positive-feedback that mediates self-organization. Specifically; since surface run-off is higher on slopes, we expect the feedback to be stronger here compared to flats.

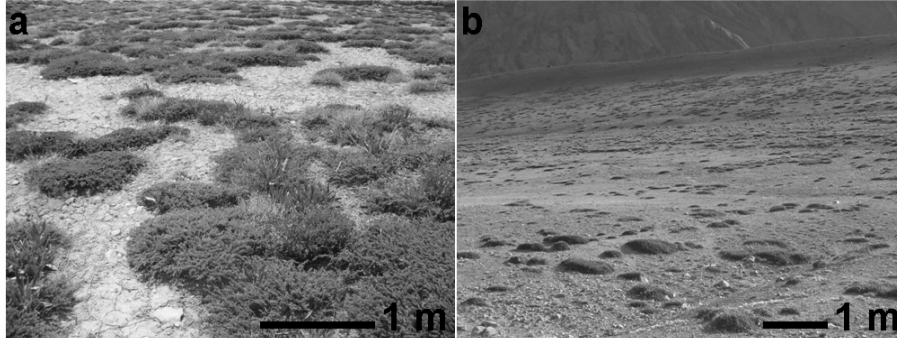


FIG. 1. Vegetation on two landscapes in Kibber Wildlife Sanctuary, Trans-Himalayas, northern India with clear demarcation between vegetated and bare patches. On sloping terrain, vegetation forms maze-like labyrinths (a); while in flat terrain it forms isolated and clustered spots (b).

Here we provide empirical test of this hypothesis by showing vegetated patches on slopes exhibit a resource concentration mechanism via strong positive feedback, which is much weaker on flat terrain. We show that vegetation on slopes retain soil moisture more effectively than adjacent barren patches, compared to similar settings on flat terrain. Since the same suite of plant species are found on both landscape categories, we also show that such modulation of positive-feedback at the plant-soil interface and the resultant resource concentration mechanism requires different plant strategies in terms of biomass allocation above and below-ground.

THEORY AND PREDICTIONS

It has been useful to this consider positive feedback mechanisms using zero-isoclines of plant density and water availability as a phase plane (Edelstein-Keshet 1988). Fig. 2 represents the isoclines graphically, and analytical details for this representation can be found in Rietkerk and van de Koppel (1997).

Plant isocline is vertical since production requires a minimum resource concentration, independent of plant density (Armstrong and McGehee 1980, Tilman 1982) and this threshold level increases under grazing. In absence of a positive feedback, the soil water isocline has negative slope at all plant densities (Fig. 2a). But, feedback mechanisms (Fig. 2b) produce a hump in the water-isocline (Rietkerk and van de Koppel 1997). An important consequence of the humped isocline is in the response of plants to grazing intensity. Now, grazing can potentially lead to an unstable equilibrium at low plant density (Fig. 2b). Since this unstable equilibrium lies between two alternative attracting stable equilibria (one with high plant density and the other with no plants, Fig. 2b), the ecosystem can undergo catastrophic shifts and become stably degraded depending on grazing pressures (Rietkerk et al. 1997). From the phase planes, it is also seen that in absence of feedbacks, soil water concentration under vegetation cover is lower than in a barren patch ($W_3 > W_2$ in Fig. 2a). Whereas, in the presence of feedbacks the reverse is expected ($W_2 > W_4$ in Fig. 2b). Given this background, we predict that positive feedbacks operating on slopes are stronger than on flats and the underlying resource concentration mechanism leads to more efficient water retention on slopes compared to flats. Thus, landscape is predicted to modulate the feedback mechanisms at the plant-soil interface.

Also, given that the same suite of plant species occurs on both terrain categories (see *Results*), how is this positive feedback established? If there are significant landscape effects, then plant strategies such as relative biomass allocation above and below ground may also depend on terrain. Specifically, biomass allocated belowground as a fraction of total plant biomass may be higher on slopes compared to flats.

METHODS

We measured soil moisture with paired plots in a vegetated and an adjacent bare patch (20-25 cm away) on 8 sloping and 6 flat rangelands of Kibber Wildlife Sanctuary (32° N, 78° E), northern India. These rangelands are part of the vast Trans-Himalayan grazing ecosystem with elevation between 4300 and 4500 m, and annual precipitation of 200 mm. The rangelands are grazed by wild herbivores (bharal, *Pseudois nayaur*, and ibex *Capra sibirica*) alongside various livestock (yak, cattle, yak-cattle hybrids, donkey, goat and sheep). Paired observations of volumetric water content (VWC as %) in the rooting zone were made using a 20 cm long,

time domain reflectometry probe (TDR, Spectrum Technologies Inc., Plainfield, USA). In the first phase of sampling, VWC was measured during the middle of the growth season in late June (2006). A second round of sampling was done at the same sites 48 hours after rain showers in early July that brought c. 30 mm of rains. Difference in VWC between these paired observations were analyzed using general linear models (GLM) in SAS v. 9.1 (SAS Institute, Cary, USA) with landscape category (2 levels, flat and sloping) and rainfall (2 levels, before and after) as blocks in a 2-way ANOVA. In this way, a significant interaction term between landscape category and rainfall would imply that ability to retain moisture depends on landscape and hence indicate landscape control over plant-soil positive feedbacks. Sampling was replicated across 8 sloping rangelands ($20^\circ - 30^\circ$ inclination) and 6 flat rangelands ($0^\circ - 5^\circ$ inclination). Paired observations of VWC were made from these locations ($n = 127$ paired samples) in late June and again in early July ($n = 139$ paired samples), 48 h after showers. Three competing models were assessed over the extent they accounted for total variation seen in the data. In the first GLM, difference in VWC between a vegetated patch and paired adjacent barren patch was analyzed with 2-way ANOVA. In the second GLM, local site conditions were incorporated by standardizing the difference in VWC relative to average VWC at a location as $(VWC_{\text{vegetated}} - VWC_{\text{barren}})/0.5(VWC_{\text{vegetated}} + VWC_{\text{barren}})$. In the third GLM, average VWC at a site was introduced as a covariate (ANCOVA).

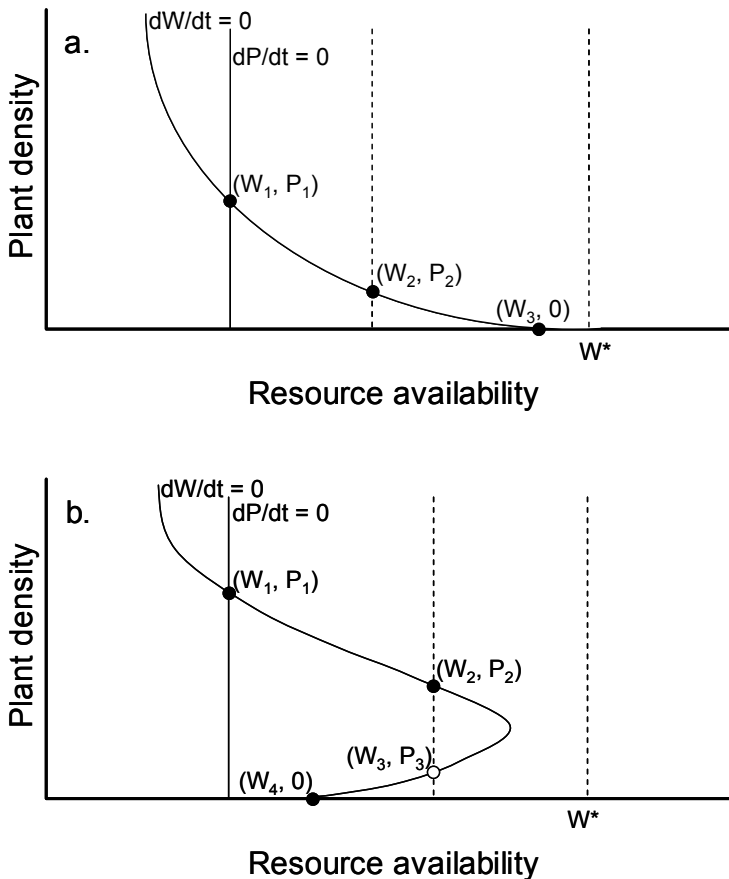


FIG. 2. Zero-isoclines for plant density ($dP/dt = 0$) and resources ($dW/dt = 0$ for soil water) as a phase plane (modified from Rietkerk and van de Koppel 1997). Solid circles are stable equilibrium points, open circles are unstable. (a) Isoclines without positive feedbacks between plants and soil. W_1 is the minimal resource concentration required for plant production with corresponding vertical plant isocline and a stable equilibrium point (W_1, P_1) . Grazing pushes this isocline to the right (dotted vertical lines). Moderate grazing establishes a stable equilibrium with low plant biomass (W_2, P_2) . Overgrazing leads to a state without plants $(W_3, 0)$ where $W^* \gg W_3$ may be the critical threshold for recovery. (b) Phase plane with positive feedback leading to a hump in the resource isocline. Under moderate grazing there are now 2 possible equilibrium points. A stable one at high plant density (W_2, P_2) and an unstable one at low plant density (W_3, P_3) . The unstable equilibrium can trigger catastrophic shifts between the vegetated state and a degraded state $(W_4, 0)$. As in (a), overgrazing leads to a degraded state with $W^* \gg W_4$. Thus, systems with feedbacks are especially susceptible to catastrophic shifts. The phase plane predicts that without feedbacks as in (a), $W_3 > W_2$. But with feedbacks as in (b) $W_2 > W_4$. This prediction is tested with field data.

During the second round of sampling, biomass allocation above and belowground was also estimated. Aboveground biomass was clipped to ground level from 0.25 X 0.25 m quadrats. Belowground biomass was collected using a 2.5 cm radius, 20 cm long, soil core from the center of each quadrat ($n = 2$ samples from each rangeland). Subsequently, the soil cores were washed in running water using 1 mm sieves to

separate all belowground plant tissues (including roots, rhizomes and scaly layers) from adhering soil. Samples were oven dried to obtain dry weight. The relative allocation of biomass belowground was calculated as $\text{Biomass}_{\text{below}} / (\text{Biomass}_{\text{above}} + \text{Biomass}_{\text{below}})$ and compared between samples from slopes and flat terrain with 1-way ANOVA.

We measured the apparent differences in ‘connectedness’ of vegetation on slopes and flats using nearest neighbor distances (Muller-Dumbois and Ellenberg 1974). Distance to 10 closest neighbors was measured from a randomly chosen focal individual. Distances were measured between the centers of canopies to the nearest cm ($n = 1$ series of measurements from each rangeland). Patterns from these data were assessed graphically.

One month after the rains, we conducted a small scale irrigation experiment on 1 slope and 1 flat, and data on VWC were collected as before. Five plots (1 X 2 m) at both locations were irrigated with 5 liters of water and $n = 2$ paired measurements were taken before and 48 hours after irrigation. These data were analyzed with GLMs as before.

RESULTS

Twelve plant species were encountered during sampling (*Caragana versicolor*, *Cousinia thomsonii*, *Dracopcephalum heterophyllum*, *Eurotia ceratoides*, *Heracleum thomsonii*, *Arnebia euchroma*, *Artemisia maritime*, *Elymus nutans*, *Leymus secalinus*, *Stipa orientalis*, *Lindelofia anchusoides* and *Astragalus rhizanthus*). None of these species were exclusive to either slopes or flats. Nearest neighbor distances depicting patterns of ‘connectedness’ of vegetation on slopes and flats are summarized in Fig. 3. Two aspects are evident: (i) in general, distance between neighbors is less on slopes, and, (ii) the trend is staircase-like in slopes compared to a smooth linear pattern on flats. These data emphasize that vegetation on slopes is more ‘connected’ than on flats.

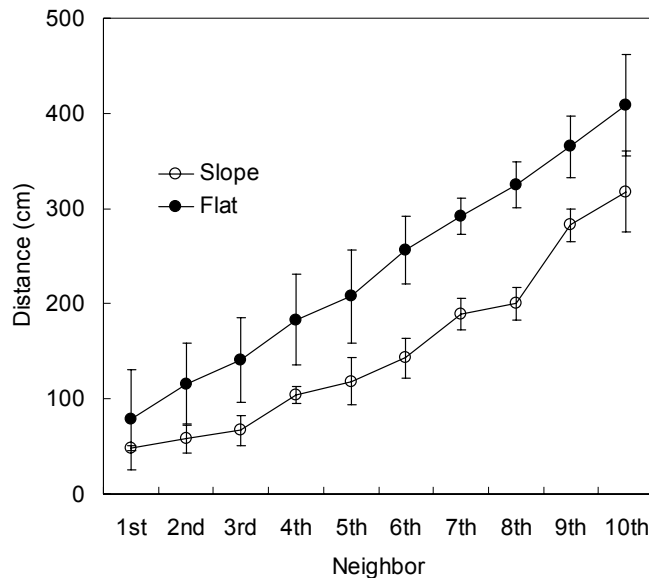


FIG. 3. Patterns of nearest neighbor distances of plants from two terrain categories (means and ± 1 SD). Distances were measured from a randomly chosen focal individual for the ten closest individuals. The data show that distances increase in a step-wise manner in slopes, compared to a linear increase over flat terrain. Also, corresponding distances are smaller on slopes compared to flat terrain. This suggests that plants are more ‘connected’ on slopes compared to being more ‘isolated’ on flat terrain.

Mean VWC before and after rainfall was 9.6% ($\pm 0.3\%$ SE), and the observed differences water retention between flat and sloping terrain are summarized in Fig. 4. Initially, VWC was lower in vegetated patches compared to the paired bare patch in both terrain categories. This difference can be attributed to the transpirational and other metabolic activities of plants. This initial net negative balance was recovered following rainfall; but, the extent of recovery differed between the two landscape categories (Fig. 4). Results from the 3 competing GLMs for VWC are in general agreement with regards to the interaction between landscape and rainfall (Table 1). But the third GLM (with covariates) explained the greatest proportion of variance in the data (indicated by $(SS_{\text{Total}} - SS_{\text{Error}}) / SS_{\text{Total}}$, Table 1). The significant ‘Landscape X Rainfall’ interaction term suggests that ability to retain soil moisture depends on terrain and this is greater on slopes compared to flats.

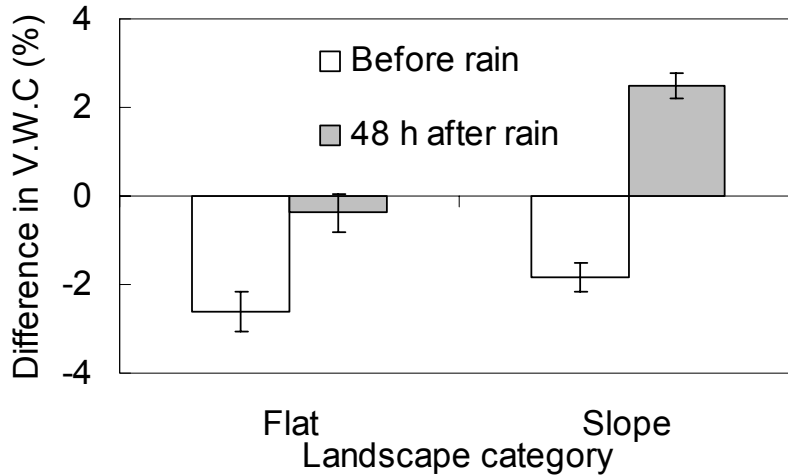


FIG. 4. Difference in volumetric water content of soil (VWC as %) between paired vegetated and barren locations from 2 landscape categories (slope and flat), before and after rainfall in rangelands of Kibber Wildlife Sanctuary, northern India (means and ± 1 SE). Initially, transpiration and other metabolic activities cause lower soil moisture for vegetated patches compared to neighboring bare areas. This net negative balance is recovered following rainfall, but the extent of recovery is greater on slopes compared to flat terrain. See text for statistical details.

Patterns of biomass allocation above and belowground are summarized in Fig. 5. The relative allocation of biomass belowground in flat terrain was 54.3% ($\pm 3.9\%$ SE) compared to 68.3% ($\pm 3.4\%$ SE) on slopes ($F_{1,26} = 7.35$, $P = 0.012$).

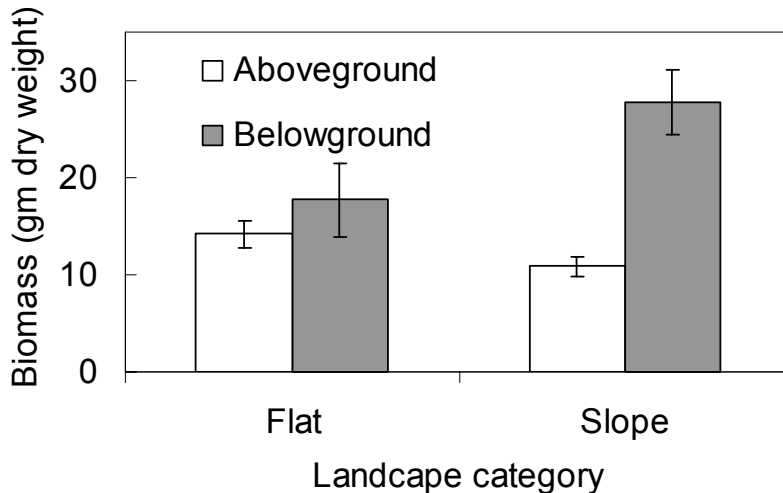


FIG. 5. Patterns of biomass allocation above and belowground in plants on 2 landscape categories from Kibber Wildlife Sanctuary, northern India (means and ± 1 SE). Data for aboveground biomass are from 0.25 X 0.25 m quadrats and for belowground biomass are from 2.5 cm radius, 20 cm long, soil cores at the center of each quadrat.

Mean VWC during the irrigation trials was 15.4% ($\pm 0.6\%$ SE). As before, the third GLM (with covariate) explained the greatest fraction of total variance in the data. Results from irrigation were similar to those from rainfall ($F_{1,33} = 4.31$, $P = 0.045$; for the 'Landscape X Irrigation' interaction term).

DISCUSSION

Results from VWC indicate that vegetation on slopes initiates a strong resource concentration mechanism, making them more efficient in retaining soil moisture compared to vegetation on flat terrain. And, results from rainfall were reproduced through irrigation trials. So, patchiness observed on slopes is self-organized and is driven by a strong positive feedback at the plant-soil interface. Whereas, it is possible that no positive feedback exists over flat terrain, or, it is much weaker. In many ways, the patterns we document in Trans-Himalayas are similar to the semiarid savannas of east Africa, where factors creating local patchiness were also related to topography (Augustine 2003), emphasizing the remarkable similarities between the world's grazing ecosystems (Frank et al. 1998).

Given this 2-phase mosaic, vegetation on slopes is more susceptible to alterations in grazing intensity and reaching a stably degraded state (Fig. 2b) compared to vegetation on flat terrain (Fig. 2a). So, regulating grazing intensity on slopes is of greater importance than on flat terrain from a sustainable management perspective, as indicated by the data on biomass allocation. While about half of plant biomass was belowground in flat terrain, this proportion approached 70% on slopes. Thus, the resource concentration mechanism for

efficient water retention corresponds with proportionally higher biomass allocation belowground on slopes. Plants invest more in belowground tissues when growing on slopes from which arises the resource concentration mechanism, but making slopes more susceptible to overgrazing compared to flats. This assertion can have profound implications for land management and sustainable use as there is accumulating evidence from around the world that grazing ecosystems are being stably degraded, thus, compromising ecosystem functions as well as services for human livelihoods (Daily 1995).

TABLE 1. Results from three competing general linear models (GLM) for analyzing differences in soil water retention in vegetated and paired adjacent barren patches among two landscape units (slope and flat) before and after rainfall from different rangelands in Kibber Wildlife Sanctuary, northern India. In the first GLM, the difference in VWC between a vegetated patch and paired adjacent barren patch was analyzed with 2-way ANOVA. In the second GLM, local site conditions were incorporated by standardizing the difference in VWC relative to average VWC at a location as $(VWC_{\text{vegetated}} - VWC_{\text{barren}}) / 0.5(VWC_{\text{vegetated}} + VWC_{\text{barren}})$. In the third GLM, average VWC at a site was introduced as a covariate. The third GLM is seen to explain the greatest amount of variance in the data based on $(SS_{\text{Total}} - SS_{\text{Error}}) / SS_{\text{Total}}$. The significant interaction between landscape and rainfall indicates that terrain modulates the positive feedback operating at the plant-soil interface.

	Source	df	SS	MS	F	P
Model 1	Landscape	1	188.44	188.44	22.58	<0.001
	Rain	1	616.56	616.56	73.87	<0.001
	Landscape X Rain	1	62.82	62.82	7.53	0.006
	Error	262	2186.68	8.35		
	Total	265	3361.98			
Model 2	Landscape	1	1.33	1.33	18.53	<0.001
	Rain	1	5.93	5.93	82.51	<0.001
	Landscape X Rain	1	1.95	1.95	27.06	<0.001
	Error	262	18.84	0.07		
	Total	265	32.56			
Model 3	Covariate	1	147.70	147.70	24.10	<0.001
	Landscape	1	30.59	30.59	4.99	0.02
	Rain	1	16.07	16.07	2.62	0.10
	Covariate X Landscape	1	144.03	144.03	23.50	<0.001
	Covariate X Rain	1	283.38	283.38	46.24	<0.001
	Landscape X Rain	1	198.60	198.60	32.41	<0.001
	Error	259	1587.20	6.12		
	Total	265	3361.98			

Pastoralism has been the major livelihood in Trans-Himalayas for millennia, and is increasingly coming into conflict with objectives of conservation and sustainable management (Bagchi et al. 2004). The data presented here have very high implications for land management in the light of recent socio-economic and socio-political changes that have led to widespread overstocking of rangelands (Mishra et al. 2001). Directional vegetation community change and land degradation are also being documented in many places (Tong et al. 2004, Bai et al. 2004). These data highlight the importance of implementing grazing strategies in the Trans-Himalaya, an important but little-known grazing ecosystem of the world. At present, apart from certain traditional herding practices that are slowly eroding (Mishra et al. 2003), there is little emphasis on managing grazing in this ecosystem. These data stress the formulation of sound management strategies based on developing knowledge of alternate vegetation states from various parts of the world (Ellis and Swift 1988, Friedel 1991, Laycock 1991). As in east African savannas, (Augustine 2003), better understanding of factors responsible for local patchiness will be critical for retention of water (and nutrients) within the ecosystem, and the resilience of these rangelands during droughts.

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