

Influence of environmental factors and sheep grazing on an Andean grassland

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Abstract

Chronic overgrazing in the central Andes alters vegetation and may cause erosion and loss of productivity, but quantitative studies are lacking. We measured the relative influence of environmental factors and sheep grazing on local plant species composition, diversity, and soil organic matter in a remote site in northwestern Argentina. Using redundancy analysis, we found that environmental variables explained 22% of variation in species composition between sites, while grazing-related variables explained 24% of variation. The complete model, incorporating all significant variables, explained 33% of variation. Aspect, season of grazing (wet vs. dry) combined with total vegetative cover, and soil type formed the basis for the first 3 ordination axes. Unpalatable or toxic species and very low-growing species were significantly more abundant on heavily grazed sites compared to relatively protected sites. Stocking rate in wet season pastures was negatively correlated with total cover, forage volume, soil organic matter, and species richness. Season of grazing had a more dramatic effect on total cover, forage volume, species diversity and soil organic matter, which were all significantly lower in wet season pastures compared to dry season pastures. Season of grazing and aspect interacted strongly: wet season pastures on north aspects appear more susceptible to degradation and changes in species composition than south-facing sites. Our results suggest that protecting pastures during the summer rainy season may be an important complement to traditional management efforts to reduce stocking rates.

Key Words: Andes, grazing effects, plant ecology, ordination, pastoralism.

This research was supported by a 1996-1997 Fulbright fellowship and 1998 N.S.F. Pre-doctoral fellowship to P.B.A. Authors wish to thank Dr. C. Reboratti of the Universidad de Buenos Aires, Ing. R. Neuman and Dr. A.R. Bianchi of INTA, Ing. L. Novara of the Universidad Nacional de Salta, and especially the people of the village of Nazareno for invaluable help and friendship. Special thanks to Ing. A. Sulekik for determining the grass species. Dr. H.R. Grau, Dr. W.K. Lauenroth, Dr. J. Powell, and 3 anonymous reviewers provided helpful comments on early drafts of the manuscript.

Manuscript accepted 11 Nov. 1998.

Resumen

El sobrepastoreo crónico en los Andes centrales altera la vegetación y puede llegar a causar erosión y pérdida de productividad. En el noroeste de Argentina estudiamos la influencia relativa de factores ambientales y pastoreo por ovejas en la composición y diversidad de plantas, y contenido de materia orgánica en el suelo. Usando una combinación de ordenamientos directos e indirectos, encontramos que las variables ambientales explicaron 22% de la variación en la composición de especies entre sitios, mientras que 24% fue explicado por variables relacionadas al pastoreo. Considerando todas las variables significativas se explicó 33% de la variación. Los 3 primeros ejes del ordenamiento estuvieron formados por exposición temporada de pastoreo (húmeda vs seca) junto con cobertura vegetal, y tipo de suelo. Las plantas tóxicas o no palatables, y plantas muy bajas, fueron significativamente más abundantes en sitios con mucha presión de pastoreo. En sitios pastoreados durante la época húmeda, la presión de pastoreo estuvo negativamente correlacionada con la cobertura vegetal total, el volumen de forraje, materia orgánica del suelo y riqueza de especies. La temporada de pastoreo tuvo un efecto más fuerte; los sitios pastoreados durante la temporada húmeda tuvieron menor cobertura total, volumen de forraje, diversidad de especies y materia orgánica en el suelo que los sitios pastoreados en la época seca. La temporada de pastoreo y la exposición interactuaron fuertemente; los sitios pastoreados durante la temporada húmeda en pendientes con exposición Norte parecen más susceptibles a degradarse y a cambiar en composición de especies que los sitios con exposición Sur. Nuestros resultados sugieren que proteger las pasturas durante el verano lluvioso puede ser un complemento importante de los esfuerzos por reducir la carga animal.

Overstocking of Andean rangelands is thought to cause increased erosion (Harden 1993, Molinillo 1993) and loss of productivity (Eckholm 1975, Parker and Alzérreca 1978). Selective grazing, especially by sheep, is usually invoked as the mechanism driving changes in species composition through the replacement of palatable species by coarse bunchgrasses (Ellenburg 1979, Ruthsatz and Fisel 1984). These problems affect virtually all Central Andean highlands

(Ellenberg 1979, Fjeldsa and Kessler 1996). However, rigorous quantitative studies of the effects of grazing on vegetation and soils are lacking; for example, a review of well over 200 worldwide studies on the effects of grazing on vegetation and soils did not include a single study from the Andes (Milchunas and Lauenroth 1993).

Traditional range management relies heavily on adjustments of the stocking rate to manipulate vegetation condition. Yet the existence of non-reversible changes caused by intense grazing (Biswell 1956, Archer 1989) demonstrates problems with this approach. Current work on non-equilibrium systems suggests that stocking rate may not be the most important determinant of vegetation condition (Ellis and Swift 1988, Westoby et al. 1989). In fact, Turner (1993) found overstocking to be a very poor predictor of degradation potential in an African pastoral system. Especially in arid and semi-arid climates subject to high interannual variation in rainfall, abiotic and stochastic processes may influence ecosystem processes (Biondini and Manske 1996) and vegetation (Wiens 1984, West 1988) far more than biotic interactions such as herbivory.

In light of these findings, management practices should consider the impact of grazing on vegetation relative to other sources of variation. McIntyre and Lavorel (1994) provided a model for studying how an exogenous disturbance overlays patterns of vegetation related to the physiographic environment. Working in a semi-arid Australian rangeland, they used canonical correspondence analysis to quantify the amount of variation in species composition explained by environmental versus disturbance variables. They also identified significant associations between individual plant species and various environmental and grazing-related factors.

McIntyre and Lavorel's (1994) approach allows us to describe the vegetation of a poorly studied grassland community in the Andes of northwestern Argentina while simultaneously quantifying the local impact of intense sheep grazing. Specifically, we aim to 1) determine the relative influence of grazing and environmental variables on

plant species composition, and 2) show the effect of grazing on individual plant species and on stand-level variables such as total cover, species richness, and soil organic matter.

Methods

Study Area

The Cordillera Oriental of northwestern Argentina is remote and undeveloped, an extremely rugged area (Fig. 1)

where subsistence remains the most important economic activity (Reboratti 1996). Few studies have examined the transitional grasslands between cloud forests and high desert, the focus of human activity in the region. Viera and Menéndez (1981) mapped geomorphic features and vegetation from aerial photos and Mendiola (1996) described plant species composition.

The study area surrounds the village of Nazareno in Salta province (22°30'S, 65°70'W) located at an elevation of 3,000 m. (Fig. 2). The site is influenced



Fig. 1. The valley of the Río Nazareno and the village of Cuesta Azul, at the southern end of the study area.

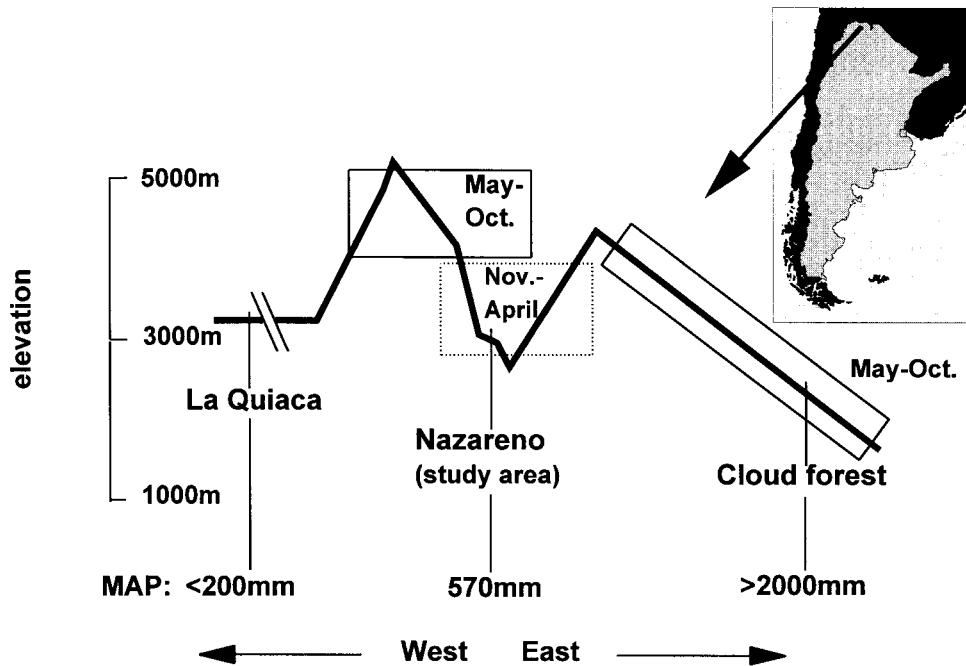


Fig. 2. Location of study site in northern Salta province, Argentina, and schematic elevation profile showing annual precipitation and pastoral movements.

by strong elevation and precipitation gradients. From October through April, the austral summer, air traveling westward from the Atlantic rises up the east slope of the Andes, drops most of its moisture over the rain and cloud forests, then becomes progressively drier. Mean annual rainfall declines from 2,000 mm at 1,000 m elevation at the eastern edge of the Andes to less than 200 mm in La Quiaca, on the Puna, or Altiplano (Bianchi 1981). Nazareno, in between these 2 extremes, receives 574 mm/yr⁻¹ (pers. comm. EVARSA, a regional utility). Seasonality is extreme, with virtually all rainfall occurring between October and April. Inter-annual variation in rainfall is low; in the 7 years of data available for Nazareno, annual rainfall ranged from 490 mm to 640 mm. Total precipitation during the study year was 597 mm, slightly above the mean. Frosts are frequent from April to October (Bianchi 1981). Steep slopes and weak sedimentary rock make the area highly susceptible to erosion and mass movement (Viera and Menendez 1981). Soils are shallow, rocky lithosoles with little organic material (Nadir 1990). The texture is sandy-loam with a high percentage of gravel, although within the study area deep pockets of clay-loam are frequent as well. Vegetation is characterized by large perennial bunch grasses

(especially *Stipa* and *Festuca* species), interspersed with scattered shrubs such as *Baccharis*, *Adesmia*, and *Senna* species.

Pastoral System and Stocking Rates

Most pastoralists near Nazareno follow a transhumant strategy in response to seasonal fluctuations of forage availability. Women or children move the family's herd of typically 50 to 150 sheep and goats to the high mountains following the harvest, then to the montane forests during the winter dry season, before returning to their villages for the summer wet season (Fig. 2). The variety of movements makes generalization difficult, and some families graze their sheep and goats year-round near their permanent home in the valley. This study focuses solely on the valley pastures surrounding Nazareno and its neighboring villages.

Almost all rangelands in the valley are communal in a legal sense, but each family retains rights through long-standing tradition to a particular sector usually surrounding their home. These zones of roughly 50 ha (with great variation) may overlap, but their boundaries are recognized and respected. Scattered within this heavily grazed matrix are small areas of natural vegetation contained within fences built to protect agri-

cultural fields from livestock, or to maintain dry season forage reserves. Not grazed until after the harvest in May, these protected sites are exceptions to the widespread wet season grazing in the valley and were sampled as "dry season" sites. They range in size from 1 ha to approximately 20 ha and are composed of the same vegetation as the adjacent "wet season" pastures.

Sheep are the dominant form of livestock, though horses, burros, and cattle are common. Our estimations of stocking rates include only sheep grazing for the following reasons: first, because horses graze very close to the houses, and cattle generally high in the mountains or near the cloud forests, sheep are the principal grazers on most of the valley rangelands. Second, since sheep are taken to pasture every day by a shepherd and are confined to the family's sector, their movements can be easily mapped, in contrast to the free-ranging cattle. Based on conversations with the pastoralists, most families have maintained a fairly constant herd size for at least a generation. Our study therefore concerns the effects of historical, rather than single-year, sheep grazing.

To calculate stocking rates during the wet season, we collaborated with workers from a livestock production program initiated by the Spanish missionary

organization OCLADE (Obras Claretianas para el Desarrollo). These extension workers showed us each pastoralist's grazing sector and supplied census information on the size and composition of their herd, and the length of time the animals remain in the sector each year. This information was supplemented by informal interviews with the pastoralists. Using aerial photos to estimate the surface area of each sector, we calculated the number of sheep and goat days per hectare. Before further statistical analysis, we divided the stocking rate (sheep and goat-days ha⁻¹) by a logarithm of the distance between the corral and the sampling site, assuming grazing intensity within each sector decreases with distance from the corral.

We were unable to calculate stocking rate for the dry season sites. Grazing on these small pastures is generally concentrated in an intense pulse during the 3 or 4 weeks following harvest and all species—horses, burros and cattle, in addition to sheep and goats—are present. Therefore, our analysis of the effect of stocking rate is limited to the subset of sites grazed during the wet season, while that of the effect of season of grazing includes all sites.

Vegetation Sampling

We sampled in upland natural grasslands extending 10 km north and 8 km south from the village of Nazareno, on the west side of the Río Nazareno. We attempted to minimize site-to-site variation in altitude, which would otherwise be the dominant influence on vegetation in this high-relief landscape (sampled sites ranged from 2,914 to 3,383 meters above sea level). Sites fall into 2 broad land-use categories: pastures grazed during the summer wet season and pastures grazed only during the winter dry season. Between January and March of 1997, fifty-seven plant surveys were completed along a trail contouring at a relatively even elevation on small east-west trending ridges. In general, we sampled 1 site on both the north and the south aspect of each ridge, locating the site subjectively in a patch of the most representative vegetation. Forty sites were located in summer wet season pastures; 17 sites were located in winter dry season pastures. At the time of sampling, dry season pastures had not yet been grazed.

We measured species composition and cover using 2 paired 10-meter line intercept transects, recording the cover of all plant species, rock, and bare ground. The parallel transects, 10 meters apart, ran with the slope, to cross the ubiquitous stock trails at a 90° degree angle. Botanical nomenclature follows Cabrera (1977–1983). We also estimated the average height of all plant species on each transect. Environmental variables including aspect (2 classes: north and south), slope, and elevation were measured. A sample of the first 10 cm of soil was collected from between the transects. Soil samples were analyzed for organic carbon and total organic material at the Instituto Nacional de Tecnología, Agropecuaria (INTA) in Cerrillos, Salta, using a wet combustion method (Walkley and Black 1934). Before samples were prepared for analysis, technicians classed soil texture qualitatively.

Information on palatability of plant species was gathered from pastoralists and Fernandez et al. (1992). "High" palatability indicates species always consumed. "Medium" describes plants which may be palatable at only 1 time of the year (usually at the start of the growing season) or eaten only in the absence of more palatable alternatives. "Poor" palatability is reserved for species that are minimally consumed and toxic species. The large number of species for which we had no information were excluded from this analysis. Using plant height and cover we calculated biovolume, a proxy for biomass (dePietri 1992). The biovolume of palatable species was summed to yield "forage volume."

Data Analysis

Ordination techniques can be used to characterize community level responses to environmental and disturbance variables, as well as to identify species sensitive to particular factors. Ordination axes can be constrained as linear combinations of a priori defined or measured variables associated with species records. As in general linear models, these variables can be combined in a stepwise manner (ter Braak and Prentice 1988). To further test independence, ordinations can be conducted after the effects of a variable or set of variables has been removed (partial analysis, Borcard et al. 1992, Okland and Eilertsen 1994).

To decide whether to use eigenvector techniques based on unimodal or linear species responses, we made scatter plots of species abundance and some of the environmental gradients, and considered the "length of gradient" measured in standard deviation units obtained by detrended correspondence analysis (DCA). After judging by eye that most species showed nearly linear responses within the observed range, and having obtained relatively short gradients in DCA ordinations (always less than 3 SD), we decided to use redundancy analysis (RDA) as our constrained ordination technique.

In the CANOCO version of RDA the fraction of the total variation in the species matrix "explained" by a variable or set of variables can be directly read from the sums of constrained eigenvalues (Jongman et al. 1987, Borcard et al. 1992). We used 99 unrestricted permutations of the constraining variable (Monte Carlo test in CANOCO, ter Braak 1990a) to assess the statistical significance of each variable. The terms "explanation" and "variation explained" are used here in a statistical sense rather than implying cause and effect. As infrequent species of random occurrence can give rise to spurious effects (Jongman et al. 1987), we excluded from the analysis species with frequency lower than 5% (66 taxa excluded, 115 included). All cover data were log-transformed to prevent high-cover species from disproportionately influencing the analysis.

To study the effects of environment and grazing we followed McIntyre and Lavorel (1994). First, we looked for significant structuring of the species data in relation to environmental variables and their interactions (aspect: north or south; soil type: clay-loam or sandy-loam; slope; elevation). Second, we quantified the effects of the grazing-related factors (stocking rate in wet season pastures; season of grazing: wet or dry; total vegetative cover; soil organic matter; date of sampling). "Grazing-related factors" are either management practices, variables directly affected by grazing, or, in the case of date of sampling, a rapidly changing variable in comparison to the "fixed" environmental factors. Third, we put both environmental and grazing factors into 1 complete model and used partial ordination to study the effects of grazing regime once environmental effects had been taken into account. In

each model, variables were included in forward stepwise selection after satisfying a Monte Carlo test.

Since Redundancy Analysis (RDA) is a form of multivariate multiple regression the results of the analysis include regression coefficients and associated t-values. An objective way to identify individual species significantly correlated with explanatory variables in RDA is by examining the t-value biplots, which are 2-dimensional graphs showing the t-values of the regression coefficients for a given species on the explanatory variables (ter Braak 1990b). We used this technique to classify species according to their association with environmental and grazing related factors. All analysis were performed using the program CANOCO version 3.12 (ter Braak 1987, 1990a).

To evaluate the effect of stocking rate (wet season pastures only) on stand-level variables, we performed a rank transformation of stocking rate, then used Spearman rank order correlations. To test differences in these variables caused by season of grazing and aspect, one-way ANOVA was used. We tested the relationship between

Table 1. Test of significance of explanatory variables for species composition. "Variation Explained" = eigenvalue of constrained axis divided by the sum of all eigenvalues. Variables included in the complete model are shown in boldface, with percent variation explained once incorporated in the model in brackets. P=significance probability of the constrained axis in a Monte Carlo permutation test (H_0 =influence of variable not significantly different from random).

Variables	Variation Explained	P
a. Environmental variables		
Elevation	2.0	0.66
Aspect	10.2 (8.0)	0.01
Soil	6.4 (6.1)	0.01
Slope	4.3	0.01
Elevation*Aspect	11.2	0.10
Elevation*Soil	8.5	0.07
Elevation*Slope	2.5	0.04
Aspect*Soil	18.8	0.01
Aspect*Slope	13.3	0.01
Soil*Slope	10.7	0.01
Aspect*Soil+Slope	21.6	0.01
b. Grazing-related variables		
Date (day of sampling)	4.6 (2.5)	0.02
Season (of grazing)	9.4 (4.5)	0.01
Stocking rate (sheep-days/Ha)	7.8	0.01
Total cover	10.2 (4.7)	0.01
Soil organic matter	7.1	0.01
Cover+Season+S.O.M.+Date	23.6	0.01

Table 2. Eigenvalues of the first 4 axes in the complete model RDA and correlation coefficients with the environmental and grazing variables. Total=sum of all eigenvalues. Boldface indicates the factor most strongly correlated with each axis.

	Axis 1	Axis 2	Axis 3	Axis 4	Total
Eigenvalue	0.1142	0.1032	0.0571	0.0388	0.332
Aspect	-0.8292	0.3649	0.3792	0.1628	
Soil Type	-0.3566	-0.0117	-0.9242	0.1019	
Date (of sampling)	0.0825	0.5490	0.0488	-0.2210	
Season of Grazing	-0.2312	-0.9006	0.0564	0.2454	
Total Cover	0.6347	0.7126	-0.0053	0.2856	

grazing response and species palatability and stature with a non-parametric ANOVA (Kruskal-Wallis H) using species' scores from the ordination. For these tests we used SPSS 8.0 for Windows and rejected the null hypothesis at $P < 0.05$.

Results and Discussion

Effects of Environmental Variables on Species Composition

Each environmental factor except altitude, which we limited to a range of less than 400 m, explained a small but significant proportion of variation in species performance (Table 1a). Aspect accounted for the highest inter-site variability in species composition (see Appendix for species list). A total of 19 species were recorded exclusively in sites facing south but only 4 species were found exclusively in sites facing north. Soil type was ranked second in amount of variation explained. Eight species were found exclusively at sandy-loam sites and 4 species were recorded only at clay-loam sites.

The combination of aspect and soil type explained 19% of total variation. In this ordination, the first axis separates north and south aspects, while the second axis separates sandy-loam from clay-loam soils. After incorporating the combined effects of aspect and soil type, the only environmental variable that could significantly increase the amount of variation explained was slope. The "best fitting" model based on environmental variables accounted for 22 % of total variation (Table 1a).

Effects of Grazing-related Factors

Differences in total vegetation cover and season of grazing were the most important factors accounting for variation in species composition. Stocking

rate and season of grazing had similar explanatory power when taken independently (Table 1b). However, once the effects of season of grazing were incorporated into the model, stocking rate was no longer significant. The model incorporating all significant variables (cover, season, organic matter, and date of sampling) explained 24% of the total inter-site variability in species composition. This value is slightly higher than the best fitting environmental model.

In this ordination of grazing-related factors, the first axis related to the contrast between total cover and season. High cover sites correlate with sites protected during the wet season, low cover sites correlate with sites grazed during the wet season. The second axis was associated with organic matter content, and the fourth axis was dominated by date of sampling. The first 2 axes accounted for 79% of the total (24%) variation explained by the set of grazing related variables.

The importance of grazing relative to environmental factors attests to the intensity of land-use in this landscape. In fact, we may have underestimated the influence of land-use due to a lack of information on 2 potentially important sources of variation, historical grazing patterns and the traditional use of fire to stimulate early season growth.

Combined Effects of Environmental and Grazing Factors

The complete model, which incorporates in a stepwise manner both environmental and grazing related variables, accounted for 33% of the total variation in the species matrix (Table 2), similar to comparable studies (Lavorel et al. 1991, McIntyre and Lavorel 1994). In this ordination the first axis is related to aspect, the second axis captures variation related to season of grazing and

Table 3. Individual species affected significantly (t-value biplot score ≤ 1) by season of grazing in the complete model RDA.

Family	Species	T-value Biplot	Variation Explained %	Palatability
a. Wet Season Pasture Species				
Apiaceae	<i>Bowlesia cf. pulchella</i> Wedd	-0.476	23.09	unknown
Asteraceae	<i>Baccharis multiflosculosa</i> Heering	-0.484	17.07	poor
Poaceae	<i>Stipa ichu</i> (R. et P.) Kunth	-0.625	14.28	poor
Poaceae	<i>Nasella pampagrandensis</i> (Spreng.) Barkworth	-0.695	10.21	poor
Oxalidaceae	<i>Oxalis argentina</i> Knuth	-0.702	9.78	medium
Asteraceae	<i>Achyrocline ramosissima</i> Sch. Bip.	-0.740	10.04	unknown
Pteridophyta spp.		-0.885	7.72	poor
Convolvulaceae	<i>Dichondra sericea</i> v. <i>microcalyx</i> Sw.	-0.887	6.76	medium
Poaceae	<i>Sporobolus indicus</i> (L.) R. Br.	-0.904	8.21	poor
Poaceae	<i>Bromus catharticus</i> Vahl.	-0.907	5.26	high
Fabaceae	<i>Senna alata</i> (L.)Rox.	-0.909	7.94	medium
b. Protected Site Species				
Asteraceae	<i>Tagetes minuta</i> Linn.	0.462	18.65	medium
Poaceae	<i>Diplachne dubia</i> (HBK) Scribn.	0.598	17.18	high
Asteraceae	<i>Stevia minor</i> Gris.	0.624	11.84	medium
Poaceae	<i>Lycurus phalaroides</i> Kuntze	0.628	15.55	unknown
Poaceae	<i>Paspalum humboldtianum</i> Flugge	0.695	13.78	high
Oxalidaceae	<i>Hypseocharis tridentata</i> Griseb.	0.730	10.39	high
Asteraceae	<i>Gutierrezia mandonii</i> Sch. Bip.	0.786	9.19	medium
Asteraceae	<i>Hypochoeris elata</i> Wedd.	0.854	5.37	medium
Poaceae	<i>Botriochloa</i> sp.	0.897	7.71	medium
Convolvulaceae	<i>Ipomoea minuta</i> f. <i>minuta</i> R. Fries	0.925	7.92	poor
Poaceae	<i>Muhlenbergia rigida</i> (HBK) Trino	0.944	5.07	medium
Poaceae	<i>Deyeuxia tarmensis</i> Pilg.	0.977	4.54	medium
Poaceae	<i>Festuca</i> spp.	0.984	4.76	medium

total cover, while the third axis represents variation due to soil type. Except for covariation of total cover with both aspect and season, the primary 3 factors (aspect, season, and soil type) are largely orthogonal (Table 2).

Partial ordination of grazing related factors once the environmental factors were taken into account explained 16% of the species matrix. This implies that one-third (8% out of 24%) of variation explained by grazing related factors was structured in the environmental matrix. Again, total cover and season were the most important variables.

Effects on Individual Species

T-value biplots indicated that species were significantly associated with grazing (Table 3) and environmental factors (see Appendix). Perennial grasses were particularly sensitive to wet versus dry season grazing. *Stipa ichu* (R. et P.) Kunth and *Nasella pampagrandensis* (Spreng.) Barkworth were indicators for sites grazed in the wet season, while *Diplachne dubia* (HBK) Scribn., *Lycurus phalaroides* Kuntze, *Paspalum humboldtianum* Flugge and *Festuca* spp. were characteristic of dry season pastures. If associations with total cover are

also considered, the highly palatable *Trifolium amabile* Kunth, a very common species, should be added to the list of indicators for dry season or lightly grazed sites.

In a non-parametric 1-way analysis-of-variance, individual species scores on the grazing-related axis 2 of the com-

plete ordination were significantly related to palatability (Table 4). The rank means for the medium and high palatability classes were similar, while the rank mean for the poor palatability class was much lower. Low-growing species were significantly more common on the heavily-grazed sites (Table 4). This effect was strongest when species less than 7 cm were compared to all taller species, and became insignificant when the limit of the short class was moved up to 15 cm.

These results support the prevailing view in the Andes that changes in species composition due to grazing are driven by differential palatability. As previous research has indicated, *Stipa ichu*, a typical coarse, unpalatable bunchgrass, is characteristic of heavily-grazed wet season pastures (Ellenburg 1979, Ruthsatz and Fisel 1984). Avoidance of highly unpalatable and toxic species appears to be more important than selection of highly palatable species, which were treated no differently than species of medium palatability.

The shift in composition to plants of lower stature on heavily-grazed sites suggests other possible mechanisms for differential response to grazing. Plants able to grow very low to the ground either avoid grazing, or have superior physiological responses to grazing compared to taller plants. Other studies in the Andes (Wilcox et al. 1987) and elsewhere (Noy -Meir et al. 1989, Belsky 1992) have identified the same pattern.

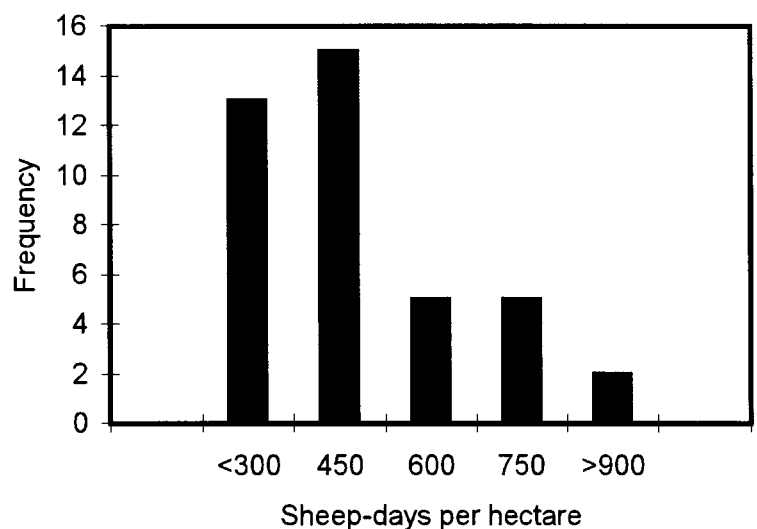


Fig. 3. Frequency distribution of stocking rates among the 40 wet season pastures.

Table 4. Palatability and plant stature affect species' scores on the grazing related axis II of the complete ordination in non-parametric one-way ANOVA (Kruskal-Wallis H.) The effect of plant stature weakens as the limit between the short and tall class is increased.

Variable and Class	N	Mean Rank	χ^2	P
Palatability				
Poor	21	28.6	6.22	.05
Medium	38	40.9		
High	17	45.3		
Plant stature				
<7 cm	41	46.2	7.92	.01
>7 cm	74	64.5		
<15 cm	72	54.1	2.62	.11
>15 cm	43	64.5		

Table 5. Spearman Rank Order Correlations among variables in wet season pasture site (n=40).

Variables	Spearman R	t (n-2)	P
Stocking rate & Total cover	-0.54	-3.95	.01
Stocking rate & Richness	-0.36	-2.41	.02
Stocking rate & Soil organic matter	-0.37	-2.41	.02
Stocking rate & Forage volume	-0.25	-1.62	.11
Total cover & Richness	0.61	4.69	.01
Total cover & Soil organic matter	0.58	4.42	.01
Total cover & Forage volume	0.58	4.41	.01

Table 6. Differences between dry season (n=17) and wet season (n=40) pastures, using one-way ANOVA.

Response Variable	Mean Dry Season Sites	Mean Wet Season Sites	F	P
Total cover (%)	133.0	67.0	51.42	.01
Forage (cm ³)	1501.0	208.0	42.01	.01
H (Shannon-Weiner)	3.9	3.5	7.46	.01
Soil organic matter (%)	4.3	3.1	4.18	.05
Richness	39.5	35.9	2.33	.13

Table 7. Mean percent cover and standard error of the mean (in parentheses) of important vegetation classes grouped by site aspect and season of grazing. Sample sizes are as follows: wet season*N=20, wet season*S=20, dry season*N=9, dry season*S=8.

Aspect	Cover class	Wet season	Dry season
(%)			
N	Grasses	27.1 (4.5)	62.3(5.8)
	Forbs	16.4 (2.6)	49.9 (6.7)
	Shrubs	8.7 (2.4)	15.6 (4.8)
	Ferns	1.4 (0.4)	0.5 (0.2)
	Bare ground	43.2 (4.3)	6.2 (3.2)
S	Grasses	40.1 (3.1)	65.2 (6.7)
	Forbs	20.2 (2.1)	39.7 (5.7)
	Shrubs	19.6 (5.5)	31.7 (6.1)
	Ferns	1.5 (0.4)	0.2 (0.1)
	Bare ground	18.4 (2.7)	3.0 (1.2)

We could not confirm the significance of plant growth form (dePietri 1992) in determining species-level response, nor do we have data on species' physiological response. Fine-scale spatial relationships may be important as well: palatable species seemed to "hide" under larger shrubs.

Stand-level Variables

The mean stocking rate in wet season pastures was 362 sheep and goat-days ha⁻¹ each 6 month wet season, and ranged from 154 to 793 (Figure 3). The Spearman rank order correlations show significant inverse relationships between stocking rate in wet-season pastures and total cover, species richness, soil organic matter and forage volume (Table 5). Total cover is positively correlated with richness, soil organic matter, and forage volume (Table 5). Total cover may be as effective as stocking rate as an indicator of site condition.

Differences between wet season and dry season pastures are dramatic. Dry season pastures have much higher total cover, forage volume, plant species diversity, and soil organic matter (Table 6). Season of grazing did not significantly affect richness.

Aspect had a strong effect on stand-level variables, consistent with its influence on species composition. Forage volume, total cover, species richness and soil organic matter were much higher in wet season pastures on south aspects compared to north aspects (one-way ANOVA, n=40, all F's >8.00, all P <.01). In dry season pastures, only soil organic matter was significantly higher on south aspects (n=16, F=6.06, P =.026). This apparent interaction between aspect and season of grazing (Table 7) led us to revisit our analysis of species composition. In the complete model Redundancy Analysis (RDA), an aspect*season of grazing interaction explained over 3% of variation in species composition even when aspect and season were included as covariables

Such a marked contrast between north and south slopes may not only be due to differences in solar radiation, but also to condensation from low clouds carried by the prevailing southerly winds in the summer wet season. These páramo-type grasslands have been termed "cloud pastures," analogous to cloud forests (Brown and Grau 1993), and unmeasured precipitation may be considerable,

especially on southern aspects. South facing slopes, which probably receive and retain more water than north slopes, are apparently more resistant to degradation caused by wet season grazing.

The Importance of Season of Grazing Compared to Stocking Rate

Whether or not a site is grazed during the summer wet season, when vegetation is active, emerged as a critical determinant of both species composition and stand-level variables. Because we have no data on stocking rates during the dry season, it is possible that dry season grazing intensities are much lower than in the wet season, meaning that difference between wet and dry season pastures would be essentially a difference in stocking rate. Given the very small size of the dry season pastures and the intensity of land-use in the area, this seems unlikely. The shorter length of rotation could also explain the lesser impact of dry season grazing. However, previous work has shown that the effects of sheep grazing on vegetation do in fact depend on the season of grazing (Bork et al. 1998). The importance of protecting vegetation during the season of active growth and reproduction has been reported in other grazing systems as well (Bartolome 1993, Brown and Stuth 1993).

We can suggest a number of mechanisms for the severe impact of wet season grazing. Many species are only palatable during the early growing season and would be avoided in the dry season (Molinillo and Monasterio 1997), making it likely that less biomass is removed during dry season grazing. Trampling is more damaging when plants are active and soil wet and soft (Heady and Child 1994). Resulting soil compaction can dramatically alter hydrology, lowering infiltration and raising sediment production (Warren et al. 1986). Grazing during the reproductive season also can cause seed loss (Bertiller 1994). Finally, soil nutrient status, which may influence species composition (Tilman 1990), would be affected by both biomass removal and increased erosive action.

Stocking rate in the wet season was less effective than both season of grazing and total cover in explaining variation in species composition and differ-

ences in stand-level variables. Clearly, the difficulties of measuring stocking rate in this complex, fenceless landscape hamper prediction. Without better estimations of stocking rate during both wet and dry seasons, we cannot exclude stocking rate as an important factor. However, it is possible that as Turner (1993) found in Africa, stocking rate may simply be a poor indicator of degradation potential.

Management Implications

Proposed management solutions in the Andes have generally focused on the need to reduce the total number of stock (LeBaron et al. 1979). Our findings suggest that protecting grasslands during the rainy season should at least complement if not significantly improve upon strategies based on reductions in stock. For example, we might suggest that the traditional annual rotation of herds through the landscape (from valley to cloud forest to high peaks) could be altered between years, allowing the valley pastures to rest in one rainy season, and the high peak pastures to rest in another. A second alternative to provide wet season protection would require further concentrating grazing pressure in some areas in order to rest others. If already degraded pastures prove stable under increased use, a reasonable possibility given the area's history of degradation, and if rested pastures do indeed recover, then the benefit of protecting one pasture might outweigh the cost of concentrating grazing on another pasture.

However, we present these alternatives pessimistically. The subsistence requirements of poor rural communities in the Central Andes, combined with environmental and cultural constraints, severely limit the potential for any management change (Browman 1987). Altering transhumant patterns, as we suggest in our first alternative, would force shepherds and their flocks to endure harsh, wet conditions among the peaks while missing Christmas and Carnival in the valley villages, the most important social reunions of the year. Protecting areas within the wet season pastures, as in our second alternative, may be impossible without fences or the capital to construct them. On the other hand, the dramatic cultural and economic transformations affecting this region, initiated by greater integration with the

national and global economy (Reboratti 1996), may generate novel perspectives and foster new approaches.

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See appendix on page 480 and 481.

Appendix. Frequency of occurrence, F(%), of plant taxa recorded in 57 sites in Nazareno, Depto. Santa Victoria, Salta, Argentina, from January through March, 1997. Species with a frequency less than 7% were not included in the ordination and are not listed. Associations of taxa with environmental and grazing factors as indicated by RDA are as follows: Aspect: N=North, S=South; Soil type: Cly=Clay-loam, Sdy=Sandy-loam, Phenology: -Phe=early, +Phe=late; Grazing regime: Wet=wet season pasture, Dry=Dry season pasture; Total cover: +Cov=high cover, -Cov=low cover.

F	Species	class	F	Species	class
(%)			(%)		
86.0	<i>Bidens pseudocosmos</i> / <i>B.exigua</i> Sherff	N, +Cov	29.8	<i>Nasella mucronata</i> (HBK) Pehl	
86.0	<i>Trifolium amabile</i> Kunth	+Cov	29.8	<i>Stenandrium dulce</i> Car.	
78.9	<i>Dichondra sericea</i> v. . <i>microcalyx</i> Sw	N, Cly, Wet, +Cov	28.1	<i>Bowlesia</i> aff. <i>pulchella</i> Wedd.	Wet, +Cov
78.9	<i>Plantago tomentosa</i> Lam.	S	26.3	<i>Astragalus garbancillo</i> Cav.	N, Cly
78.9	<i>Stipa ichu</i> (R. et P.) Kunth	Wet, +Cov	26.3	<i>Cynodon hirsutus</i> Stent.	
71.9	<i>Tagetes pusilla</i> Humb.	N, Sdy	26.3	<i>Gamochaeta subfalcata</i> Cabr.	
66.7	<i>Eragrostis andicola</i> Fries	N, Sdy	26.3	<i>Iridaceae</i> sp.	
66.7	<i>Rebunium richardianum</i> Gillies	S	24.6	<i>Adesmia</i> aff. <i>cytisoides</i> "A" Griseb.	S, +Phe
64.9	<i>Microchloa indica</i> (Lif.) P. Beauv.		24.6	<i>Chondrosium simplex</i> (Lag.) Kunth	N, +Phe
63.2	<i>Oxalis argentina</i> Knuth	S, Wet	24.6	<i>Crassulaceae</i> sp.	
57.9	<i>Muhlenbergia rigida</i> (HBK) Trino	N, Sdy	24.6	<i>Erodium cicutarium</i> (L.) L'Hér. ex Aiton	
52.6	<i>Hypochoeris elata</i> Wedd.	S, Dry	24.6	<i>Hypseocharis tridentata</i> Griseb.	N, Dry
49.1	<i>Bromus catharticus</i> Vahl.	S, -Phe, Wet, +Cov	24.6	<i>Pennisetum chilense</i> (Desv.) B.D. Jackdon ex R.E. Fr.	+Cov
49.1	<i>Stevia minor</i> Gris.	Dry	24.6	<i>Satureja parviflora</i> (Phil.) Epling	S
47.4	<i>Elyonurus muticus</i> (Spreng.) Kuntze	Sdy	24.6	<i>Tagetes minuta</i> Linn.	Dry
45.6	<i>Nasella pampagrandensis</i> (Spreng.) Barkworth	S, Wet, +Cov	22.8	<i>Parthenium hysteriophorous</i> L.	N, Cly
45.6	<i>Poa</i> sp.	S	21.1	<i>Achyrocline ramosissima</i> Sch. Bip.	Sdy, Wet, +Cov
43.9	<i>Ipomoea minuta f.minuta</i> R. Fries	Dry	21.1	<i>Lepechinia meyenii</i> Walp.	Sdy
42.1	<i>Cheilanthes pruinata</i> Kaulf.	Sdy	21.1	<i>Lycurus phalaroides</i> Kuntze	Dry
42.1	<i>Cyperus andinus</i> Palla ex Kuk	S	21.1	<i>Sisyrinchium chilense</i> Hook.	
42.1	<i>Richardia stellaris</i> Cham.	N, Sdy	21.1	<i>Viguiera tucumanensis</i> Hook.	
40.4	<i>Allium</i> spp.	S	21.1	<i>Zinnia peruviana</i> (L.) L.	
40.4	<i>Hypochoeris meyeniana</i> v. <i>meyeniana</i> Walp	Cly, +Phe, -Cov	19.3	<i>Adesmia</i> aff. <i>cytisoides</i> "B" Griseb.	N, Cly
38.6	<i>Bidens mandonii</i> Sherff	N	19.3	<i>Chloris halophila</i> Parodi	N, +Cov
38.6	<i>Festuca</i> spp.	S	19.3	<i>Drymaria cordata</i> (L.) Wild. Ex Roem. et Schult.	N
36.8	<i>Arenaria lanuginosa</i> (Michaux) Rohrb.		19.3	<i>Nierembergia andina</i> Millán	
36.8	<i>Belloa punae</i> Cabr.	S, +Phe	19.3	<i>Stipa</i> sp.	
36.8	<i>Pteridophyta</i> spp.	Sdy, Wet, +Cov	17.5	<i>Amicia medicaginea</i> Griseb.	Sdy
35.1	<i>Galinsoga unixioides</i> Gris.	+Cov	17.5	<i>Baccharis polifolia</i> Gris.	
33.3	<i>Aristida adscensionis</i> v. <i>modesta</i> Hack.	N, Sdy	17.5	<i>Medicago lupulina</i> L.	N, Cly
33.3	<i>Deyeuxia tarmensis</i> Pilg.	S	17.5	<i>Senecio pampae</i> Ling.	+Cov
33.3	<i>Euphorbia prostrata</i> Aiton.		17.5	<i>Senna alata</i> (L.) Rox.	-Phe, Wet, +Cov
33.3	<i>Stipa pseudoichu</i> Caro	N, -Phe, +Cov	15.8	<i>Cerastrium</i> sp.	S
31.6	<i>Vulpia myuros</i> (L.) Gmel. forma <i>megalura</i> (Nutt.) Stace & Cotton	N	15.8	<i>Cyperus</i> sp.	+Cov
29.8	<i>Baccharis multiflosculosa</i> Heering	-Phe, Wet, +Cov	15.8	<i>Facelis lasioscarpa</i> Griseb.	Sdy, +Phe
			15.8	<i>Gutierrezia mandonii</i> Sch. Bip.	Cly, Dry, -Cov
			15.8	<i>Hypoxis decumbens</i> Linn.	
			15.8	<i>Balbisia calycina</i> (Griseb.) A.T. Hunz et Ariza	+Cov

Appendix Continued

F	Spe	class
(%)		
14.0	<i>Agalinis genistifolia</i> Cham. & Schltld.	S
14.0	<i>Calceolaria fabrisii</i> Botta & Cabrera	Sdy
14.0	<i>Eupatorium lorentzii</i> Hier.	S,Sdy,+Phe
14.0	<i>Gomphrena celusioides</i> Mart.	
14.0	<i>Koeleria</i> sp.	
12.3	<i>Apium</i> sp.	.
12.3	<i>Dichondra argentea</i> H. et. B.	Cly, -Cov
12.3	<i>Gentianella benedictae</i> (Gilg.) Fabris	S
12.3	<i>Solanum spegazzinii</i> Bitter	
12.3	<i>Sporobolus indicus</i> (L.) R. Br.	Wet, +Cov
10.5	<i>Aphanostelma parviflorum</i> Malme	
10.5	<i>Botriochloa</i> sp.	Dry
10.5	<i>Commelina</i> aff. <i>virginica</i> L.	-Phe, +Cov
10.5	<i>Evolvulus sericeus</i> Sw. v. <i>sericeus</i>	N
10.5	<i>Geranium sessiliflorum</i> Car.	
10.5	<i>Hieracium neofurcatum</i> Sleum.	
10.5	<i>Malaxis padilliana</i> L.O. Williams	
10.5	<i>Mutisia acuminata</i> v. <i>paucijuga</i> Gris.	-Phe
10.5	<i>Opuntia soehrensii</i> Britton & Rose	
10.5	<i>Oxalis bisfracta</i> Turcz.	S
8.8	<i>Anemone decapetala</i> Ard.	
8.8	<i>Bulbostylis</i> sp.	
8.8	<i>Hieracium dasychaetocomum</i> Zahn	
8.8	<i>Hoffmanseggia yaviensis</i>	
8.8	<i>Mitracarpus brevis</i> Schum.	S
8.8	<i>Paspalum humboldtianum</i> Flugge	Dry
8.8	<i>Peperomia peruviana</i> (Dhlst.) Miq.	
8.8	<i>Polygala mendocino</i> Phil.	
8.8	<i>Stevia lilloi</i> Rob.	
8.8	<i>Trichocline auriculata</i> v. <i>auriculata</i> Wedd.	
7.0	<i>Astragalus</i> sp.	
7.0	<i>Calycera pulvinata</i> Remy.	
7.0	<i>Conyza serrana</i> Cabr.	S
7.0	<i>Conyza spiciformis</i> Griseb.	S, +Phe
7.0	<i>Diplachne dubia</i> (HBK) Scribn.	Dry
7.0	<i>Eupatorium prassifolium</i> Gris.	
7.0	<i>Gnaphalium jujuyense</i> Cabrera	
7.0	<i>Luzula peruviana</i> Gmeln.	
7.0	<i>Muhlenbergia peruviana</i> (P. Beauv.) Steud.	Sdy, +Phe
7.0	<i>Orchidaceae</i> sp.	
7.0	<i>Primulaceae</i> sp.	
7.0	<i>Stellaria antoniana</i> Volponi	-Phe