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PLANT TRAITS AND ECOSYSTEM GRAZING EFFECTS: COMPARISON OF U.S. SAGEBRUSH STEPPE AND PATAGONIAN STEPPE

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Abstract. Plant functional traits provide one tool for predicting the effects of grazing on different ecosystems. To test this approach, we compared plant traits and grazing response across analogous climatic gradients in sagebrush steppe, USA (SGBR), known to have a short evolutionary history of grazing, and Patagonian steppe, Argentina (PAT), where generalist herbivores exerted stronger selective pressures. We measured grazing response by sampling vegetation and soils across distance-from-water gradients at arid, semiarid, and subhumid study areas in both regions. Based on a previous analysis of graminoid traits, we predicted that: (1) high forage quality in all three SGBR communities would lead to high utilization and large grazing effects, whereas low quality in arid PAT would constrain utilization and grazing impacts, with semiarid and subhumid PAT intermediate in quality and grazing response; and (2) grazing in arid PAT would cause shifts in relative abundance within the graminoid functional group, due to the large range of forage quality among graminoids, but in SGBR, where all graminoids are relatively palatable, shifts in abundance would occur between grasses and shrubs.

Utilization in locations close to water was higher in SGBR than in PAT study areas. This utilization difference led to differences in grazing effects consistent with our first prediction. Abundance of graminoids increased with distance from water in all three SGBR communities and in subhumid PAT, but not in arid PAT. Shrub and total production decreased with distance in SGBR but not PAT study areas. Grazing variables explained less variation in species composition in arid PAT (43%) than in any other study area (59–74%). Grazing did not significantly influence species richness. Evidence for our second prediction was mixed. Grazing did alter the relative abundance of SGBR graminoids and shrubs, but abundance shifts among the graminoids in SGBR communities were larger than in PAT communities, counter to our prediction.

This case study demonstrates how plant traits can explain relative effects of grazing on ecosystem structure and functioning, although predicting species-specific responses remains a challenge. Regardless of their evolutionary origin, poor-quality graminoids make the arid Patagonian steppe more resistant to overgrazing than communities dominated by more nutritious species.

Key words: aridity gradients; consumption; ecosystem structure and function; generalist herbivores; graminoid nutritional quality; grazing; Patagonia; plant traits; primary production; sagebrush steppe; species composition; species diversity.

INTRODUCTION

Domestic livestock grazing has dramatic effects on plant communities and soils in some arid and semiarid ecosystems, but only subtle effects in others (Milchunas and Lauenroth 1993). Attempts to explain this variability have used two related, but contrasting, approaches. The first approach relies on conceptual models that explain grazing response based on global or regional variation in factors such as precipitation, soil nutrient status, and the evolutionary history of grazing (Milchunas et al. 1988, Olff and Ritchie 1998). The second approach takes information about plant functional traits, specifically traits that allow plants to avoid or tolerate herbivory, and makes predictions about grazing response for particular plant communities or species (van der Meijden et al. 1988, Díaz et al. 1992, 2001, McIntyre et al. 1999, Vesk and Westoby 2001, Westoby et al. 2002).

Both approaches have strengths and weaknesses. Global conceptual models explain the ultimate causes of variation in grazing response among ecosystems, but

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can be difficult to evaluate because their primary mechanisms are implicit: selective pressures such as precipitation, nutrient supply, and evolutionary grazing history lead to the development of plant functional traits that, in turn, condition grazing response. These implicit mechanisms are rarely tested directly, and when they are, pose methodological challenges, especially in the case of evolutionary history of grazing (as in Milchunas and Lauenroth 1993). In contrast, predictions based on plant traits are easily tested, but fail to explain the origin of cross-ecosystem variation in the traits themselves, the ultimate cause of regional differences in grazing impacts.

The global conceptual models and plant traits approaches naturally fit into one framework if we state two separate hypotheses. Hypothesis 1: Variables such as precipitation, soil nutrient status, and evolutionary history of grazing, which constitute the direct evolutionary and ecological selective pressures on plants, determine plant functional traits. Hypothesis 2: Plant functional traits that influence physiological responses to defoliation, as well as herbivore nutritional status and foraging patterns, determine how grazing will affect the plant community's structure and functioning. Tests of the first hypothesis, a problem in evolutionary ecology, would compare plant traits in ecosystems with different levels of resource supply, evolutionary history, or other selective pressures. The challenge is teasing apart the simultaneous effects of many selective pressures. Tests of the second hypothesis, a problem in applied ecology and the focus of this study, require plant traits data along with observations or experiments on the effects of grazing on vegetation and soils. The challenge here is identifying key functional traits and then understanding how differences in their means and variances translate into differences in grazing response.

We tested these two hypotheses by conducting a comparative study of plant traits and grazing effects in the sagebrush steppe (SGBR) of the northwestern United States and the Patagonian steppe (PAT) of southern Argentina, ecosystems characterized by similar climates (Paruelo et al. 1995) but believed to have different evolutionary histories of grazing, with a shorter history of grazing in SGBR than PAT (Mack and Thompson 1982, Lauenroth 1998). We evaluated the first hypothesis, concerning the evolutionary origins of plant traits, in a previous study in which we tested the influence of precipitation and evolutionary grazing history on plant traits (Adler et al. 2004). We focused this analysis of traits on graminoids, the most abundant plant functional type and the primary forage resource for livestock. We measured morphological traits including height, leaf length and width, and leaf tensile strength, and chemical traits such as concentrations of silica, phosphorous, carbon, nitrogen, cellulose, and lignin.

Based on Milchunas et al. (1988), we expected to find more grazing-resistant traits in graminoids from the system with a longer evolutionary history of grazing, Patagonia, and from arid rather than more humid locations within each region. The comparison provided evidence largely consistent with this prediction (Adler et al. 2004). For example, the dominant PAT graminoids, especially those from the arid site, were much lower in leaf tissue nitrogen. In PAT, crude protein concentrations in mature green leaves of the dominant graminoids ranged from 4.5% to 4.8% at the arid site and from 5.6% to 6.3% at the subhumid site. In arid and subhumid SGBR, crude protein concentrations ranged from 6.3% to 9.4% (Adler et al. 2004). These differences in forage quality can have large consequences for animal performance because voluntary intake in ruminants often decreases when crude protein content falls below 7–10% (reviewed in Mattson 1980, Allison 1985). As crude protein content falls below this threshold, secondary production will be limited by forage quality, not forage quantity, and utilization, the proportion of available forage consumed, will decline. Low forage quality may also influence the distribution of utilization within a pasture, typically concentrated around water sources, because animals will need to forage more widely in search of the rare nutritious components of the vegetation (Redfern et al. 2003). Although these differences in plant traits supported the evolutionary history of grazing hypothesis, we could not rule out the role of alternative selective pressures. Nitrogen limitation created by the extremely coarse soils common in arid Patagonia also could be responsible for low N in tissues of arid Patagonian grasses (Adler et al. 2004).

Whether the inferior forage quality of the Patagonian graminoids represents an adaptation to a long evolutionary history of grazing or to abiotic stresses such as N limitation, we can combine the traits comparison with Hypothesis 2 to make two predictions about the relative effects of grazing on SGBR and PAT plant communities. (1) Because nutritional quality of dominant graminoids will influence utilization by livestock, we should find low levels of utilization in arid PAT, intermediate utilization in semiarid and subhumid PAT, and relatively high utilization in all three SGBR communities, at least in sites close to water sources. These differences in grazing intensity will lead to differences in the effects of grazing on plant communities and soils, with the weakest effects in arid PAT, intermediate effects in semiarid and subhumid PAT, and the strongest effects in SGBR communities. (2) Although Patagonian graminoids range from very low to high quality, the sagebrush graminoids fall in a narrower range of moderate to high quality. Therefore, we expected grazers to forage more selectively within the grass functional type in PAT, leading to a decrease in the abundance of the high-quality graminoids and an increase in the abundance of the low-quality species. In SGBR, shifts in relative abundance among the grasses should not be as dramatic, but changes in the relative abundance of

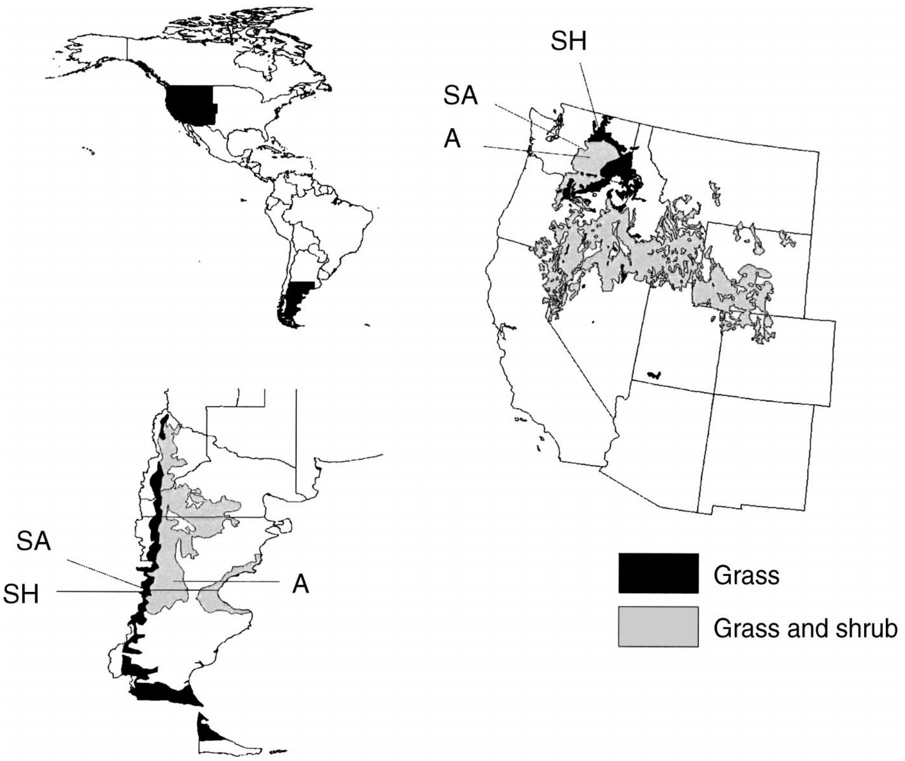

FIG. 1. Vegetation types and location of the arid (A), semiarid (SA), and subhumid (SH) study areas in the sagebrush steppe of North America and the Patagonian steppe of South America. For North America, the Grass area corresponds to Küchler's (1964) ''Fescue/Wheatgrass'' and ''Wheatgrass/Bluegrass'' vegetation types, and the Grass and shrub area is Küchler's ''Sagebrush steppe.'' For South America, the Grass area corresponds to the ''Subandean district'' and the Grass and shrub area to the ''Occidental District'' and ''Gulf of San Jorge District'' of León et al. (1998).

grasses and shrubs, the other significant component of the vegetation, should be larger than in PAT.

The global conceptual models could not have generated these predictions. The first prediction is novel because it treats utilization as a response variable influenced to some extent by plant traits, rather than as an independent variable imposed by managers. Ecosystem ecologists have recognized the importance of plant quality in regulating levels of herbivory (Mattson 1980), but this feedback seems underappreciated within the applied plant–animal interactions literature. The second prediction, about shifts in abundance within and between plant functional groups, is far more specific than predictions offered by global conceptual models, which by definition must ignore much of the heterogeneity within vegetation. The plant traits approach encourages such detailed predictions, but results are often equivocal (Vesk and Westoby 2001). By conducting our comparison in ecosystems structured by similar abiotic factors and focusing our traits analysis on one plant functional type of key importance for livestock, we hoped to increase our predictive power.

We tested the predictions by sampling across distance-from-water gradients, a proxy for historical grazing pressure, at arid, semiarid, and subhumid study areas in SGBR and PAT. To test the first prediction, concerning the magnitude of grazing effects, we collected data on consumption, utilization, and responses to grazing in primary production, species richness and composition, and soil organic matter. To test the second prediction, concerning shifts in relative abundance, we used a subset of this larger data set focused on the abundance of the graminoid and shrub functional types as well as the abundance of individual graminoid species.

DESCRIPTION OF CASE STUDY

Continental comparison

The sagebrush steppe of the Columbia Plateau of North America and the Patagonian steppe of southern South America are well matched with respect to abiotic factors. Both regions, located near 45° latitude (Fig. 1), occupy rain shadow deserts created by the Pliocene uplift of the Cascades in North America and the Andes in Patagonia (Wolfe 1969, Solbrig 1973). Pleistocene glaciations and accompanying alluvial and aeolian deposition created soils from similar granitic and basaltic parent materials (P. B. Adler, M. F. Garbulsky, J. M. Paruelo, and W. K. Lauenroth, *unpublished manuscript*). Current climate in both regions is characterized by cool winters and warm, dry summers, with precip-

TABLE 1. Information about study areas in the United States and Argentina.

Steppe type and site name	Latitude	Longitude	Elev. (m)	MAP (mm)	MAT (°C)	Soil texture
Sagebrush steppe						
Wanapum State Park (arid)	46.95° N	120.01° W	300	170	11.5	silt loam, sandy loam
Ellensburg (semiarid)	46.86° N	120.42° W	550	~250	8.6	silt loam, loam
N. Douglas County (subhumid)	48.00° N	119.30° W	800	300+	~7.5	sandy loam, silt loam
Patagonian steppe						
Río Mayo (arid)	45.39° S	70.25° W	500	154	8.6	sandy
Lago Blanco (semiarid)	45.93° S	71.37° W	600	~250	~7.5	sandy
Valle Huemules (subhumid)	45.97° S	71.53° W	650	~400	6.5	loamy sand

Notes: We refer to the three study areas within each region as arid, semiarid, and subhumid because they span a precipitation gradient, although not all sites fit the formal definition of these climate regimes (i.e., Bailey 1979). Extensive information on the arid, semiarid, and subhumid sagebrush steppe sites, respectively, is given by the following three National Resource Conservation Service ecological site descriptions for the Columbia Plateau resource area: Loamy 6–9″ Precipitation Zone (PZ), Dry Loamy 9–15″ PZ, and Cool Loamy 9–15″ PZ.

itation concentrated in fall through spring, resulting in strong climatic similarity (Paruelo et al. 1995; P. B. Adler, M. F. Garbulsky, J. M. Paruelo, and W. K. Lauenroth, *unpublished manuscript*). Vegetation reflects the similarity in climate: shrubs and caespitose C_3 bunchgrasses dominate plant communities in both regions, with grasses increasing in importance in the coolest, wettest areas (Küchler 1964, León et al. 1998: Fig. 1). A satellite-derived vegetation index demonstrated convergence in the structure and function of SGBR and PAT (Paruelo et al. 1998).

Although the climatic similarity of these two regions is demonstrated by data, our understanding of the difference in their evolutionary grazing histories relies on indirect evidence. Milchunas et al. (1988) used both systems as examples of semiarid regions with short evolutionary histories of grazing, but the presence of apparent adaptations to grazing in the Patagonian flora (Lauenroth 1998) and the grazing response of other South American temperate grasslands (Díaz et al. 1994) suggest that Patagonia may have a longer history of grazing than the sagebrush steppe. Indigenous cultures in Patagonia depended on the guanaco (*Lama guanicöe*), the wild ancestor of the llama, for food and materials for clothing and shelter. These large herbivores were abundant well into the last century, with 400 000 guanaco hides exported from Buenos Aires as late as the 1970's (Franklin 1981). In contrast, archeological and historical evidence from SGBR makes a strong case for the absence of dense populations of ungulates, at least during the Holocene. Bison were never as abundant in southeastern Washington during the last 10 000 years as they were in Montana at the beginning of the 19th century (Lyman and Wolverton 2002), and were never seen by Europeans west of the Upper Snake River Plain (Butler 1978). Mack and Thompson (1982) noted the absence of rhizomatous grasses and dung beetles in SGBR as further evidence of a lack of coevolution with grazers. The cause of such low ungulate densities was most likely a combination of low herbaceous production, occasional severe winters, barriers to recolonization from the east following local extinctions, and human hunting pressure (reviewed in Lyman and Wolverton 2002).

Study areas

In both SGBR and PAT, we selected three study areas spanning regional precipitation gradients (Fig. 1, Table 1). We focused on the portion of the SGBR within the Columbia Basin of eastern Washington State, one of the few areas of SGBR containing some locations as dry as those in arid Patagonia, and others as productive as those in subhumid Patagonia. In selecting study areas, we required large areas of native vegetation free of severe invasion, current grazing management consistent with historical management, and pastures large enough to create strong gradients in grazing intensity. Table 1 describes the location and abiotic environment at each study area (climate data are from Priest Rapids Dam, National Climatic Data Center; Daly et al. 1994, Bertiller et al. 1995, Beltrán 1997).

The arid and semiarid SGBR study areas are dominated by the perennial bunchgrasses *Pseudoroegneria spicata*, *Poa secunda*, and *Achnatherum thurberianum*, and the shrub *Artemisia tridentata* ssp. *tridentata*, whereas the subhumid SGBR community is dominated by *P. spicata*, *Festuca idahoensis*, and *Artemisia tripartita* (see Plate 1). The arid PAT community is dominated by the bunchgrasses *Stipa speciosa*, *Stipa humilis*, and *Poa ligularis*, and the shrubs *Mulinum spinosum*, *Senecio filifolia*, and *Adesmia campestris*, whereas the subhumid PAT study area is dominated by *P. ligularis*, *Festuca pallescens*, and *M. spinosum*, and the semiarid PAT study area has a mix of dominants from both the arid and subhumid communities. For clarity, we refer collectively to the vegetation of the three North American study areas as sagebrush steppe (SGBR) and the three South American sites as Patagonian steppe (PAT), even though they represent distinct community types within their respective floristic provinces (Daubenmire 1970, León et al. 1998). Botanical nomenclature follows Hitchcock and Cronquist (1973) for SGBR and Correa (1969–1999) for PAT.

TABLE 2. Grazing management at each study area.

Study area	Grazers	Season	Consumption† ($g \cdot m^{-2} \cdot yr^{-1}$)
Sagebrush steppe (SGBR)			
Arid	cattle	spring, alternate years	5
Semiarid	cattle	spring-fall, every year	13.5
Subhumid	cattle	spring/summer, alternating summer/fall	18–20
Patagonian steppe (PAT)			
Arid	sheep	continuous, every year	6.5–14
Semiarid	sheep	continuous, every year	26–30
Subhumid	sheep	continuous, every year	26–30

† For the PAT study areas, we converted stocking rate to expected consumption based on the number of sheep-days per year grazed in each pasture and an assumed intake rate of 1 kg dry matter per sheep per day. For the SGBR pastures, we used the number of animal unit months (AUMs) per pasture per year and assumed an intake of 360 kg per AUM.

Grazing management

Beginning in the mid 19th century in SGBR (Miller et al. 1994) and the early 20th century in PAT (Soriano 1983), initial development of the livestock industry in each region featured similar grazing management. Management practices in the two regions have since diverged. Sheep, once common in SGBR, are now the exception, with cattle grazing the rule. In contrast, sheep are grazed throughout PAT, and small numbers of cattle are found only in the most productive areas (Soriano 1983). A second important difference is the timing of grazing. Originally, livestock in SGBR were turned out in early spring and brought in during fall. As evidence of degradation caused by late-spring grazing accumulated (Daubenmire 1940, Laycock 1967), managers moved to shorter rotation systems or began resting pastures in alternate years. In PAT, year-round grazing is generally the norm. Stocking rates in both regions have decreased over time due to ecological concerns, reductions in forage production, and economic trends such as a decrease in the price of wool (Paruelo and Sala 1992*a*, Miller et al. 1994, Borelli 2001).

The study areas that we selected reflect these regional differences in grazing management (Table 2). First, all three SGBR study areas are grazed by cattle raised for beef production, and all three PAT study areas are grazed by sheep raised for wool. The literature suggests that spring grazing by sheep (Laycock 1967, Bork et al. 1998) and cattle (Daubenmire 1940, Rickard et al. 1975) has similar effects on SGBR vegetation, but we tested this assumption by sampling sites within a sheep pasture located close to the semiarid SGBR study area, east of Ellensburg, Washington, USA. Second, although grazing is seasonal at the SGBR study areas, it is year-round at the PAT sites. Stocking rates increase with precipitation in both regions, but are generally higher at the PAT study areas (Table 2), presumably because of the presence of productive wet meadows within these pastures. We consider the implications of these regional management differences in the *Discussion*.

METHODS

Sampling design

Water exerts a strong influence on livestock distribution in dry environments (Coughenour 1991, Bailey et al. 1996), creating gradients of grazing intensity in otherwise homogeneous vegetation, with heavy grazing occurring near permanent water sources and light grazing or no grazing occurring far from water (Valentine 1947, Lange 1969, Andrew 1988). Following previous work (Pickup et al. 1998, Turner 1998, Nash et al. 1999), we documented the degree of change in vegetation with distance from water, a measure of the cumulative impact of livestock grazing at each study area.

Along these distance-from-water gradients, we measured four sets of variables: (1) indicators of livestock grazing intensity including consumption, utilization, feces density, and a defoliation index; (2) primary production, a key ecosystem response to grazing; (3) plant species composition, which contains information on population- and community-level responses to grazing; and (4) soil organic matter, a measure of grazing impacts on long-term productive potential. In the following sections, we first explain our site selection criteria, describe methods for each of these sets of variables, and provide statistical methods.

Site selection

Within each of the six study areas, we identified three independent permanent water sources. In most cases, each water source was located in a different pasture. We used pastures in which the stocking rate and the location of water and fences had remained relatively constant over the last 20 years. We then selected 5–7 study sites at varying distances from each water source. On each transect, we attempted to hold aspect and soil type constant, and only selected sites characteristic of typical native upland vegetation (avoiding heavily invaded sites). This stratification meant that we could not use fixed distances from water. Sites were never located within the trampled, denuded areas immediately sur-

PLATE 1. Characteristic vegetation of (left) the arid sagebrush steppe and (right) arid Patagonian steppe study areas. Photo credit: P. Adler.

rounding water. When possible, we also sampled natural vegetation in long-term (>20 years) ungrazed sites, such as grazing exclosures or fenced roadsides, that were located near each transect.

Fieldwork in SGBR was carried out during the 2000, 2001, and 2002 growing seasons, and in PAT during the 1999–2000 and 2000–2001 growing seasons. In SGBR, 2000 and 2001 precipitation was 80% of normal and 2002 precipitation was 90% of normal. In PAT, precipitation was 70% of normal in 1999–2000, and 105% of normal in 2000–2001.

Consumption and primary production

At three sites on each distance-from-water transect, we built temporary 10 × 10 m exclosures in order to measure consumption and primary production. We constructed these exclosures during the dry season preceding sampling at each study area. At sites that were sampled in two consecutive years, the exclosures were not relocated. The data showed no indication that the second year of protection from grazing affected production.

We measured primary production using direct harvests inside the temporary exclosures and at the long-term ungrazed sites at the time of peak biomass (early to mid-January in PAT, late May to mid-June in SGBR). We used different procedures to estimate production of three plant functional types: (1) annuals and perennial forbs; (2) perennial graminoids, and (3) shrubs. For annuals and perennial forbs, we used a standard quadrat harvest technique. To measure the production of perennial graminoids, the group that was the focus of our plant traits analysis (Adler et al. 2004), we harvested on a per plant rather than per area basis to reduce variability caused by spatial heterogeneity. We estimated shrub production using the method of Fernández et al. (1991), calibrating their regression relationships for SGBR shrub species. These methods are described in detail in Appendix A.

To measure consumption at grazed sites with temporary ungrazed exclosures, we followed the same protocols in a grazed area adjacent to the exclosure. However, in the paired grazed sample, we only estimated forage production. We defined forage as all species in the annuals plus forbs and perennial graminoid functional types (excluding shrubs), and defined consumption as the forage production in the temporary ungrazed exclosure minus forage production in the adjacent grazed area. Utilization is consumption divided by forage production in the ungrazed area. In the arid PAT study area, shrubs and unpalatable *Stipa* grasses contribute a large portion of annual production and are consumed by livestock, but at low intensity. After failing to detect measurable consumption of the *Stipa* species and shrubs at heavily grazed sites, and finding a low frequency of defoliated leaves in *Stipa* species, we did not continue harvesting them in grazed areas. Therefore, at the arid PAT study area, our consumption and utilization measures may represent slight underestimates. We decided that moving the temporary exclosures during the growing season to minimize errors associated with changes in growth rate due to current-year grazing (Oesterheld and McNaughton 2000) was not warranted because of the short growing season and low productivity of these systems.

In addition to direct measures of consumption and grazing intensity that we carried out at grazed sites with temporary exclosures, we also used two indirect estimates of grazing intensity at all sites. First, we counted the density of livestock feces. In PAT, we counted individual fecal pellets on two 40 × 0.2 m belt transects at each site, following Fernández (1986). In SGBR, we counted fecal pats on two 40 × 1 m belt transects. Second, we used a semiquantitative measure of the frequency and intensity of defoliation (Paruelo and Sala 1992*b*). This index scores individual plants on the following scale: 0, no tillers defoliated; 1, one tiller defoliated; 2, more than one but not all tillers defoliated;

and 3, all tillers defoliated. We selected two or three dominant grass species at each study area, and averaged the scores of 10 randomly selected individuals of each of these species. We defined dominants as the one or two most abundant grazing decreasers, along with the most important grazing increaser.

Species composition

We measured the basal cover of perennial graminoids and density of shrubs on three 40-m line transects at each site. We distributed eight 1 × 1 m quadrats systematically on each of these transects, identified all plant species within each quadrat, and visually estimated percent canopy cover by species. We measured density of perennial grasses and shrubs in the 1 × 1 m quadrats, but used nested 0.5 × 0.5 m quadrats to estimate density of annual and forb species. We defined nonnative species on a continental basis.

Soils

To measure soil texture and bulk density, at all sites we extracted five soil cores of 5 cm depth from randomly selected bare-ground microsites. To measure total soil C and N at the subset of sites also sampled for production, we took additional soil cores from beneath five randomly selected perennial grasses and five randomly selected shrubs. For each site, we calculated total soil C and N as the sum of C and N per square meter in bare, grass, and shrub microsites, weighted by the proportional cover of each microsite. Detailed field and laboratory methods are given in Appendix A.

Statistical analysis

To analyze the effect of distance from water on utilization, production, composition, and soil response variables, we used mixed-effects linear models. In order to include data from the long-term exclosure sites, we transformed distance from water, a continuous variable, into a categorical variable by creating three distance classes and a fourth class for long-term exclosures. Within each study area, we defined the distance classes so as to include a roughly equal number of sites in each class (Table D1 in Appendix D). Analyses of consumption and utilization, which did not include long-term exclosure sites, permitted tests based on these distance-from-water classes as well as tests using distance from water as a continuous variable. For each response variable, we started the analysis with three fixed factors and their full interactions: (1) region, PAT and SGBR; (2) precipitation, arid, semiarid, subhumid; and (3) distance-from-water class. We included transect, nested within region by precipitation, as a random factor. We also included annual potential radiation, which integrates slope and aspect (Swift 1976), as a covariate. For soil response variables, we included soil sand fraction as a covariate as well. We removed highest order interactions and covariates not significant at $\alpha = 0.10$. We tested for significant differences among least-squares means at $\alpha = 0.05$. Note that because long-term exclosures (distance class 4) were not available at all study areas, for models in which the region by precipitation by distance class interaction was insignificant and least-square means were aggregated by region or precipitation, the least-squares means for distance class 4 are poorly estimated. We checked all residuals for normality and transformed response variables as necessary. In these cases, reported least-squares means were back-transformed (statistical tables are shown in Appendices B and C). All analyses were run in SAS 8.2 using Proc Mixed (SAS Institute 1999).

Models of production responses used 2001 growing-season data from SGBR and 2000–2001 data for PAT. For each site where two years of production data were available (SGBR arid and semiarid, PAT arid), we also constructed a mixed-effects model with distance class and year as fixed effects and transect as a random effect. We used these repeated-measures tests to confirm the results from the single-year models that included all study areas.

To compare the influence of grazing on plant species composition at each study area, we needed a multivariate approach that would not be confounded by differences in the range of environmental variation present within each study area. We chose Redundancy Analysis (RDA), a constrained ordination technique analogous to a multivariate multiple regression, because it allowed us to partition the influence of grazing and environmental variables on species composition at each study area. For each of the six study areas, we used RDA to measure the amount of variation in species composition explained by grazing variables, after first removing variation explained by environmental variables, providing an index of the overall influence of grazing on plant species composition. The environmental variables were potential radiation, elevation, sand fraction, and clay fraction, and the explanatory grazing variables were fecal count, defoliation index, distance-from-water class, and transect. We used square-root transformed canopy cover estimates of all species occurring in at least three sites in each study area as the response variables. We ran these analyses in CANOCO 4.0 (ter Braak and Smilauer 1999).

RESULTS

Prediction 1: magnitude of grazing effects

Consumption and utilization.—Forage consumption, measured by direct harvest, was significantly higher at SGBR compared to PAT study areas (statistical tables in Appendix B), despite higher pasture-wide stocking rates in PAT (see Fig. D1 in Appendix D). In fact, all consumption measurements in PAT fell below expected consumption based on pasture-wide mean stocking rates, whereas at all SGBR study areas, consumption at some sites exceeded the expected mean. At most study areas, distance-from-water class had no signifi-

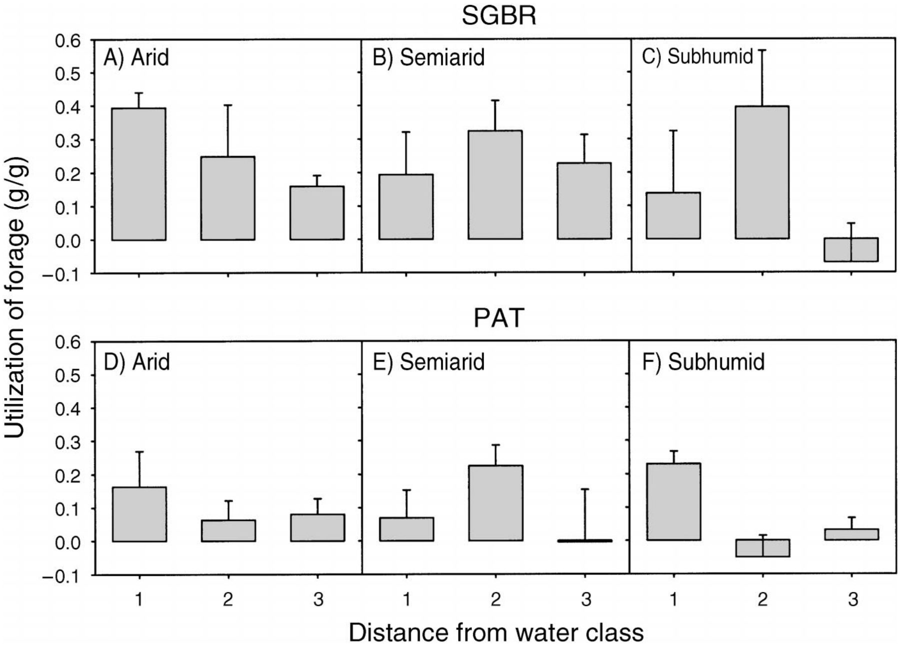

FIG. 2. The relationship between utilization (observed proportion of forage consumed; mean + 1 SE) and distance from water (by class: 1, 2, or 3). Forage is defined as all annuals, forbs, and perennial grasses. Differences among means within each study area were not significant, but utilization in sagebrush steppe (SGBR, top row) was higher than in Patagonian steppe (PAT, bottom row). See Appendix B for statistical tables. Negative values of utilization occur when forage biomass in the grazed area is higher than in the temporary exclosure.

cant effect on consumption, but at the subhumid SGBR site, consumption was highest in distance class 2, whereas at the subhumid PAT study area, consumption was highest in distance class 1. In the analysis based on distance from water as a continuous variable, a quadratic relationship emerged at all SGBR study areas and the semiarid PAT study areas, indicating that highest consumption occurred at sites located at intermediate distances from water ($F = 10.02$, df = 1, 26.2, $P = 0.004$).

Utilization, the proportion of forage production consumed, likewise was significantly higher in SGBR than PAT (Fig. 2; Appendix B). Averaged across region and precipitation gradients, utilization showed a nonsignificant decrease with distance-from-water class ($P = 0.10$). In the analysis based on distance-from-water as a continuous variable, the negative effect of distance on utilization was significant ($F = 7.94$, df = 1, 47, $P = 0.007$). Despite this negative monotonic relationship, at some study areas the individual sites with the highest utilization occurred at intermediate distances from water (Fig. D2 in Appendix D).

Trends based on indirect measures of grazing pressure, taken at all sites in each study area, were consistent with the direct measures. Values of the defoliation index in the distance class closest to water averaged 1.8, 1.6, and 1.6 at the SGBR arid, semiarid, and subhumid study areas, respectively, but only 0.8, 0.9, and 1.1 at the three PAT study areas (on a scale of 0 to 3). The defoliation index declined with increasing distance from water (correlation coefficients ranged from -0.36 to -0.87 for all study areas except semiarid PAT, where the correlation was -0.19) but, as with the direct measure of consumption, at some study areas the maximum values of the defoliation index occurred at intermediate distances. Fecal counts also declined with increasing distance from water, with the highest value occurring close to water in some pastures, and at intermediate distances in others.

Grazing effects on abundance of plant functional types.—Perennial graminoid basal cover increased significantly with distance from water at all three SGBR study areas and at the subhumid PAT study area. The increase was significant but less dramatic at the semiarid PAT study area, and there was no significant distance effect in arid PAT (Appendix B; Appendix D Fig. D3). Perennial graminoid production showed similar trends: production increased significantly with distance at the SGBR and subhumid PAT study areas, but did not respond to distance at the arid or semiarid PAT study areas (Fig. 3; Appendix B). There was no overall difference between regions, but production increased significantly with increasing precipitation. A repeated-measures test based on two years of production data at the arid PAT sites also failed to demonstrate a relationship between distance from water and total perennial grass production (Appendix C). When this test was run on palatable perennial graminoids only, excluding the *Stipa* species, production increased significantly, ranging from a least-squares mean of 5.3 $g \cdot m^{-2} \cdot yr^{-1}$ in

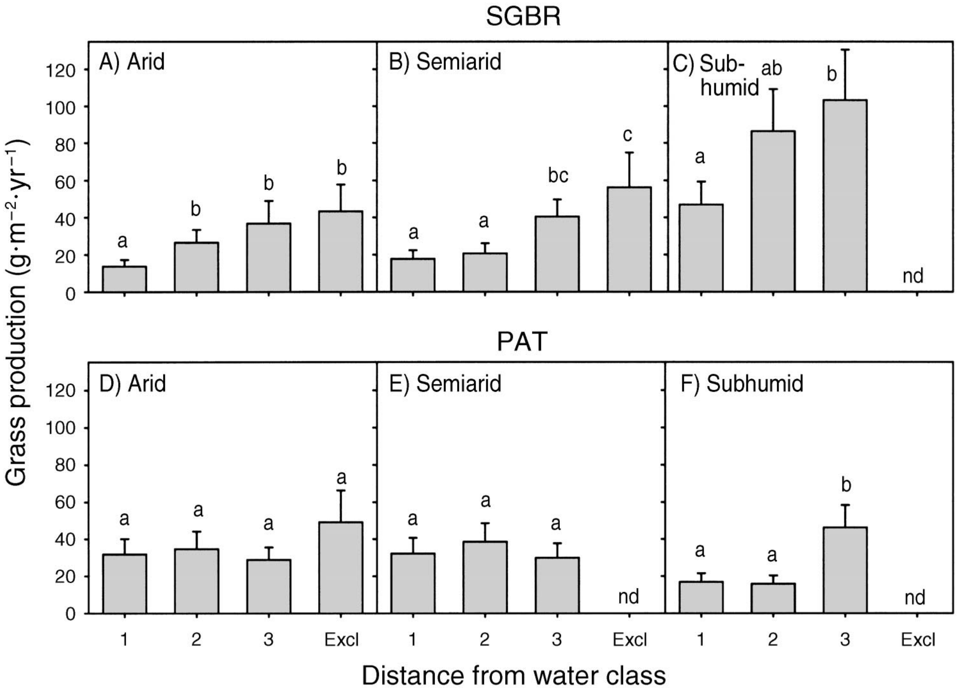

FIG. 3. Perennial grass production (least-squares means + 1 SE) as a function of distance from water at arid, semiarid, and subhumid study areas in SGBR and PAT. Within each panel, columns sharing lowercase letters are not significantly different ($\alpha = 0.05$). ''Excl'' (exclosures) refers to long-term ungrazed sites, and ''nd'' indicates that no data are available.

sites closest to water to 23.8 $g \cdot m^{-2} \cdot yr^{-1}$ in long-term ungrazed sites (Appendix C).

Shrub canopy cover was highest in sites closest to water in both regions (Appendix B). The region by precipitation interaction was significant because shrub cover was relatively constant across the precipitation gradient in PAT, but fell sharply in SGBR with increasing precipitation. Results for shrub production differed from those for shrub cover. Using one year of data, distance had no effect (Appendix B). However, the repeated-measures tests showed that shrub production was significantly higher at the locations closest to water in the arid and semiarid SGBR study areas, but distance had no significant effect at the arid PAT study area (Appendix C, Appendix D Fig. D4).

The combined production of forbs and annuals varied significantly with distance only at the arid PAT site, where the mean for long-term ungrazed sites, 8.5 $g \cdot m^{-2} \cdot yr^{-1}$, was significantly higher than the means for distance classes 1 through 3, which ranged from 0.5 to 1.7 $g \cdot m^{-2} \cdot yr^{-1}$ (Appendix B). Mean forb and annual production in arid PAT was much lower than the means at all other study areas.

Total aboveground production increased with distance from water in SGBR but not PAT (Fig. 4; Appendix B). Repeated-measures tests confirmed the regional difference in grazing response: at the SGBR arid and semiarid study areas, total production increased with distance from water, but there was no significant difference at the arid PAT study area (Appendix C). Total production increased with precipitation in a similar fashion in both regions: averaged across distance from water, means ranged from 63 and 56 $g \cdot m^{-2} \cdot yr^{-1}$ in arid SGBR and PAT, respectively, to 103 and 104 $g \cdot m^{-2} \cdot yr^{-1}$ at the subhumid SGRB and PAT study areas.

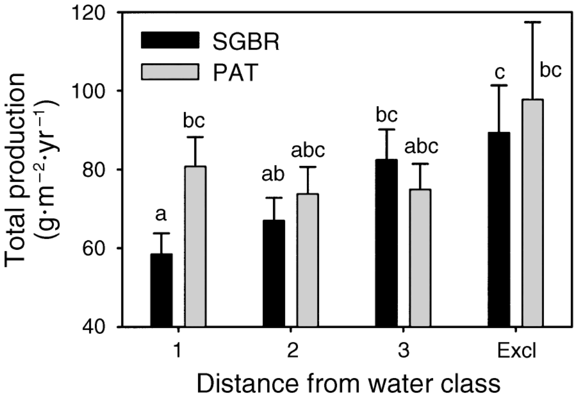

FIG. 4. Total aboveground production as a function of region and distance from water, averaged across precipitation within each region. Bars show least-squares means and +1 SE. Means sharing the same letter are not significantly different ($\alpha = 0.05$). ''Excl'' refers to long-term ungrazed sites.

Species richness and composition.—Grazing had either weak or no effects on species richness, depending on spatial scale. Averaged across region and precipitation, the effect of distance class on the number of species per 1 m^2 (the average species richness of the

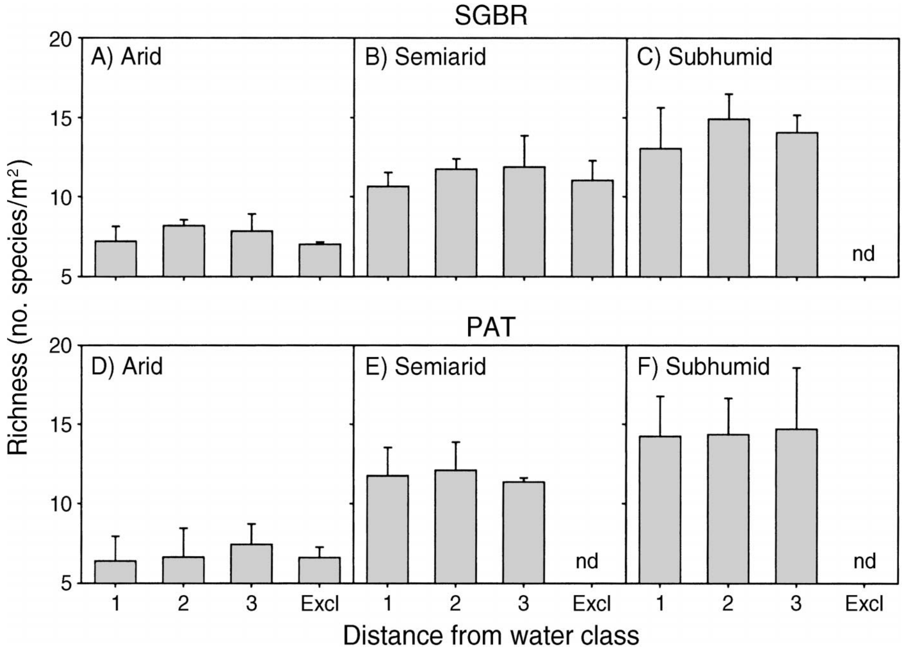

FIG. 5. Species richness (least-squares means + 1 SE) in 1-m^2 quadrats as a function of distance from water at arid, semiarid, and subhumid study areas in SGBR and PAT. Averaged across region and precipitation, differences among least-squares means for distance class were significant at $\alpha = 0.10$, with higher richness at intermediate distance classes. ''Excl'' refers to long-term ungrazed sites, and ''nd'' indicates no data.

individual 24 quadrats at each site) was marginally significant ($P = 0.089$), with peaks in species richness at intermediate distances (Fig. 5; Appendix B). Richness at this scale increased with precipitation equally in both regions. In contrast, species richness per site, the number of species found in all 24 quadrats, was unrelated to distance from water. In this case the region by precipitation interaction was significant (Appendix B), with greater increases in species richness across the precipitation gradient in SGBR than in PAT: mean richness per site in arid SGBR and PAT was 20.3 and 20.6, respectively, increasing to 40.0 and 31.6 in subhumid SGBR and PAT. Results were similar using the Shannon-Weiner diversity index as the response variable: there was a trend toward higher evenness at intermediate distances from water, and evenness increased with precipitation in both regions, but more so in SGBR than PAT (not shown).

TABLE 3. Results of redundancy analysis (RDA).

Ecosystem and study area	Variation explained (%)	RDA 1	RDA 2	RDA 3	RDA 4
Sagebrush steppe					
Arid	74	0.180	0.055	0.045	0.018
Semiarid	60	0.203	0.127	0.049	0.025
Subhumid	59	0.183	0.067	0.035	0.026
Patagonian steppe					
Arid	43	0.203	0.074	0.063	0.028
Semiarid	64	0.275	0.115	0.062	0.035
Subhumid	60	0.226	0.136	0.065	0.023

Notes: Shown is the percentage of variation in species composition explained by grazing variables in RDA axes 1–4, after accounting for variation due to environmental factors. Also shown are the eigenvalues of the first four RDA axes. Grazing variables included transect, distance-from-water class, fecal counts, and the defoliation index. Environmental variables included potential radiation (an integrator of slope and aspect), elevation, and soil texture (sand and clay fractions).

The number of non-native species per site, averaged across region, was significantly higher close to water than in more distant grazed sites, but was not higher compared to long-term ungrazed sites (Appendix B, Appendix D Fig. D5-A). More strikingly, although non-natives increased with precipitation in both regions, the number of exotics in the arid and semiarid sites was much lower in PAT than in SGBR (Fig. D5-B). The PAT data are dependable, but the SGBR data may underestimate exotic richness because of our effort to avoid sampling heavily invaded sites in that region.

Using RDA, grazing variables explained more variation in species composition at the arid SGBR study area (74%) than at the arid PAT study area (43%), after accounting for variation due to environmental covariables (Table 3). Variation explained at the semiarid and subhumid study areas was similar in both regions (59–64%). At the SGBR study areas, the dominant grasses *P. spicata* and *F. idahoensis* increased with increasing distance from water and decreasing defoliation, whereas bare ground, the shrub *A. tridentata*, the short-statured grass *P. secunda*, *A. thurberianum*, and *H. comata* were more abundant in more heavily grazed sites close to water (Fig. 6A–C, Table 4). Grazing increasers in arid (Fig. 6D) and subhumid PAT (Fig. 6F) included the shrub *M. spinosum*, the sedge *Carex andina*, *Stipa* species, and the rhizomatous *Poa lanigunosa* (one of the few common rhizomatous graminoids at any study area), whereas the grasses *Bromus pictus*, *P. ligularis*, and *F. pallescens* were associated with lightly grazed and ungrazed sites. However, at the semiarid PAT site, distance from water, fecal counts, and the defoliation index were not well correlated, making for a poorly defined grazing intensity gradient. Instead, differences among pastures (''TRANSECT'' in Fig. 6E) explained much of the variation in species composition, separating species common to arid Patagonia, such as the *Stipa* species, from species characteristic of more humid sites, such as *F. pallescens* and *F. magellanica*.

Effects of sheep grazing on sagebrush steppe.—In the one sheep pasture that we sampled in SGBR, trends with distance from water were similar to the results from the cattle pastures: grazing intensity, measured indirectly by the defoliation index and fecal pellet counts, decreased with distance from water; grass abundance increased with distance; and shrub cover decreased with distance. Consistent with results from cattle pastures, species richness at the site scale showed little variation with distance from water. However, species richness at the 1-m^2 scale increased with distance from water.

Soils.—Distance from water did not have a significant effect on total soil C or N (Appendix B). Concentrations of C and N, although variable across distance-from-water gradients, were on average lowest in bare-ground microsites at all study areas (Fig. D6). Total C and N increased with precipitation in both regions, but values at the arid and semiarid sites were higher in SGBR than PAT (Fig. 7). In a model accounting for differences in soil sand fraction, the region by precipitation interaction was significant, and the regional difference was reversed: predicted soil C was higher in PAT than SGBR after adjusting for texture (Appendix B). Results for soil N were qualitatively identical.

Prediction 2: shifts in species relative abundances

At all of the SGBR study areas, the dominant grass species in exclosures or lightly grazed sites far from water was replaced by another grass at sites close to water (Fig. 8A–C). At each of the PAT study areas, in contrast, one grass species remained most abundant across the entire grazing-intensity gradient (Fig. 8D–F).

Discussion

Prediction 1: magnitude of grazing effects

Based on our previous analysis of graminoid functional traits (Adler et al. 2004), we predicted that utilization and, in turn, the ecosystem effects of grazing would be greater in all three SGBR communities than in arid PAT, with intermediate responses at semiarid and subhumid PAT. We found strong support for both parts of this prediction.

Utilization.—As predicted, we found few differences in consumption and utilization among the three SGBR communities, which all had high forage quality. Although differences in utilization among the PAT study areas were not significant, the trend toward higher maximum utilization and defoliation in subhumid PAT, compared to the arid PAT community dominated by poor-quality grasses, is consistent with our prediction. The continental differences were also significant: utilization was significantly higher in SGBR than PAT. In fact, utilization in sites close to water in arid SGBR was more than twofold greater than in arid PAT. We found that the highest values of utilization and defoliation often occurred not in sites closest to water, but in those at intermediate distances, suggesting that distance from water is best interpreted as a proxy for historical, not current, grazing intensity (Adler and Hall 2005). Many of the grazing effects that we documented, such as decreases in perennial graminoid production near water at the SGBR and subhumid PAT study areas, could be considered indicators of overgrazing. However, these shifts in utilization away from water following severe reductions in the availability of nutritious forage near water may constitute the strongest evidence of overgrazing, because they imply increased energetic costs to livestock.

The lower utilization at the PAT study areas is paradoxical given their higher stocking rates. If PAT plants compensated more than SGBR plants following defoliation, then our utilization measurements would be biased. The results from the defoliation index allow us to reject this explanation: PAT grasses were not defoliated as frequently or intensely as SGBR grasses, especially in sites near water. A more likely explanation has to do with the presence of wet meadows in the PAT pastures, especially common in the subhumid PAT study area. These highly productive sites, although only a small portion of the total landscape, provide a large component of sheep forage (Somlo et al. 1992). The absence of wet meadows in the SGBR study areas means that upland vegetation is the primary forage resource. At the arid SGBR study area, extensive unproductive lithosols further concentrate grazing pressure on the relatively productive sites that we sampled, explaining why observed consumption was higher than expected.

The importance of wet meadows in PAT, however, does not explain why upland forage is not better utilized. With higher stocking rates or different management practices, perhaps livestock would be forced to take advantage of the apparently abundant forage in the Patagonian uplands. However, historical data suggest that these pastures are stocked to economic ca-

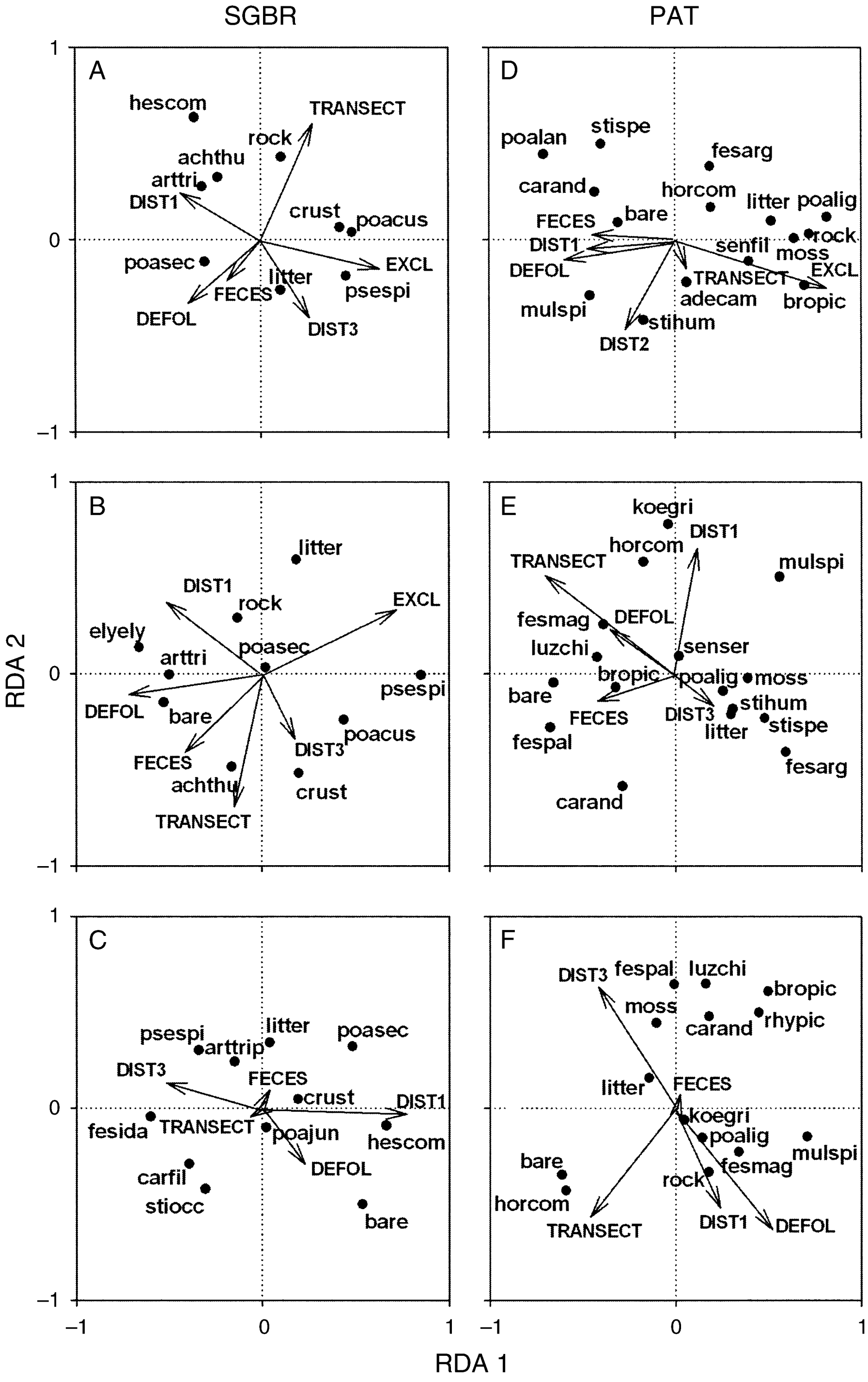

FIG. 6. Ordination results for arid, semiarid, and subhumid SGBR (A–C) and PAT (D–F) study areas. Locations in the plane [RDA 1, RDA 2] of ground cover and important perennial grass and shrub species are shown by dots and lowercase labels; locations of grazing variables are shown by arrows and uppercase labels. Species abbreviations are given in Table 4. Grazing variable codes are as follows: DIST1 and DIST3, sites in distance-from-water classes 1 and 3, respectively; EXCL, long-term exclosures or ungrazed sites; FECES, livestock fecal density; DEFOL, index of defoliation frequency and intensity; TRANSECT, distance-from-water transect replicate, usually located in separate pastures.

TABLE 4. Species name abbreviations, by study area, used in the ordinations (Fig. 6). Common synonyms are shown in parentheses.

Species code	Species name
Sagebrush steppe	
achnel	*Achnatherum nelsonii* ssp. *nelsonii* (*Stipa occidentalis v. nelsonii*)
achthu	*Achnatherum thurberianum* (*Stipa thurberiana*)
arttri	*Artemisia tridentata* ssp. *tridentata*
arttrip	*Artemisia tripartita*
carfil	*Carex filifolia*
elyely	*Elymus elymoides* (*Sitanion hystrix*)
fesida	*Festuca idahoensis*
hescom	*Hesperostipa comata* (*Stipa comata*)
poacus	*Poa cusickii*
poajun	*Poa juncifolia*
poasec	*Poa secunda*
psespi	*Pseudoroegneria spicata* (*Agropyron spicatum*)
Patagonian steppe	
adecam	*Adesmia campestris*
bropic	*Bromus pictus*
carand	*Carex andina*
fesarg	*Festuca argentina*
fesmag	*Festuca magellanica*
fespal	*Festuca pallescens*
horcom	*Hordeum comossum*
koegri	*Koeleria grisebachii*
luzchi	*Luzula chilensis*
mulspi	*Mulinum spinosum*
poalan	*Poa lanigunosa*
poalig	*Poa ligularis*
rhypic	*Rhytidosperma picta*
senfil	*Senecio filaginoides*
stihum	*Stipa humilis*
stispe	*Stipa speciosa*

pacity (Soriano and Paruelo 1990, Paruelo and Sala 1992*a*, Golluscio et al. 1998). Lambing rates at the arid and semiarid study areas currently decrease in response to increases in stocking rate (Anchorena and Cingolani 1999, Borelli 2001). Utilization and livestock production in these pastures appear to be limited by forage quality, not quantity.

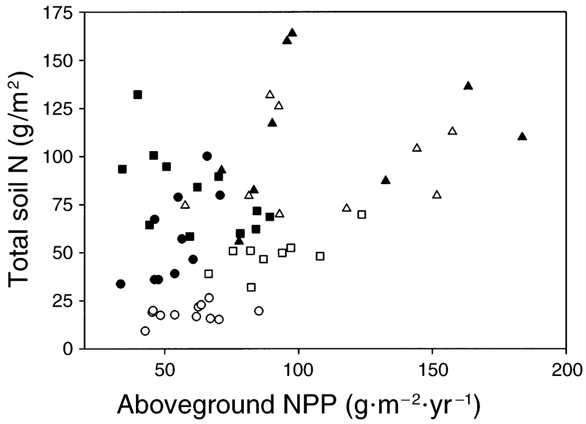

FIG. 7. The relationship between total soil N in the top 5 cm and aboveground net primary production at the six study areas. Solid symbols show SGBR study areas; open symbols show PAT. Different symbols denote arid (circles), semiarid (squares), and subhumid (triangles) study areas. Soil organic matter is lower in PAT than SGBR at the arid and semiarid sites. This difference is largely accounted for by a statistical model incorporating soil texture (soils are quite sandy at the arid and semiarid PAT study areas).

Changes in production and composition.—Consistent with our prediction, the high utilization at all three SGBR study areas caused important changes in primary production and species composition. Both perennial grass abundance, measured as cover or production, and total aboveground production increased with distance from water, whereas shrub production decreased with distance from water. The constrained ordinations based on grazing variables explained a high percentage of variation in species composition (59–74%). Within PAT, grazing response was greater at the subhumid than at the arid study area. Perennial grass abundance increased with distance from water at the subhumid but not the arid site. The percentage of variation in species composition explained by grazing variables was much higher in subhumid PAT (60%) than arid PAT (43%). Responses at the semiarid PAT study area, similar to arid PAT for some variables and similar to subhumid PAT for others, further support a trend of stronger grazing effects with increases in precipitation and forage quality. The lack of differences among the three SGBR study areas may be due to the narrower ranges of precipitation and forage quality represented, or by smaller differences among study areas in soil texture, which

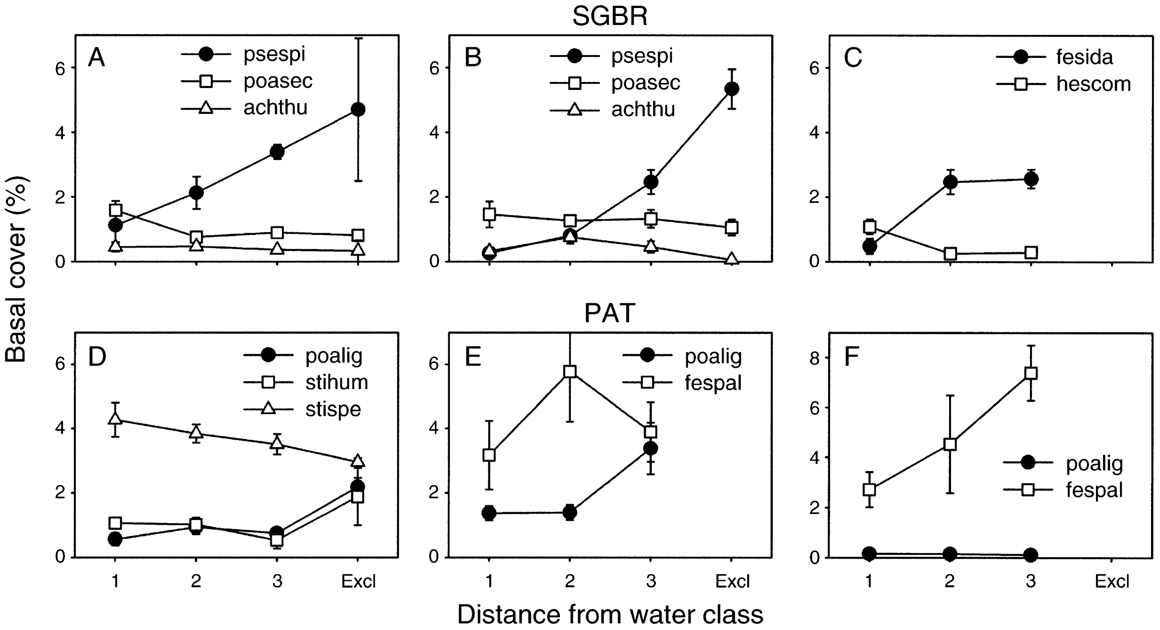

FIG. 8. Changes in the basal cover (mean + 1 SE) of the most common grass species with distance from water at each of the six study areas: (A) SGBR arid, (B) SGBR semiarid, (C) SGBR subhumid; (D) PAT arid, (E) PAT semiarid, and (F) PAT subhumid. At all SGBR study areas, but none of the PAT study areas, grazing causes a replacement of the most abundant grass species. "Excl" refers to exclosures and other long-term ungrazed sites. Species codes are given in Table 4.

can influence N availability in semiarid systems (see *Successes and limitations of the plant traits approach*).

Grazing had stronger effects in the SGBR study areas than in arid PAT, as we predicted based on lower forage quality in the PAT community. Graminoid and total production decreased with heavy grazing in all SGBR communities, but were not influenced by grazing in arid PAT. Similarly, grazing increased shrub production in SGBR but not arid PAT. The only response variable for which arid PAT showed more sensitivity to grazing than any SGBR community was production of forbs and annuals, presumably because the low quality of the dominant arid PAT grasses forces livestock to forage very selectively. The grazing response of subhumid PAT was intermediate, with grazing effects on graminoid abundance and overall species composition similar to the SGBR results, but the total production response resembled arid PAT.

Total soil C and N were not influenced by grazing in either region. The lack of response in PAT, where grazing did not affect total production, is not surprising. In SGBR, where grazing did lower total production in heavily grazed sites, the absence of a significant response in soil organic matter could be due to the slow turnover of this large pool (Burke et al. 1997), or to changes in belowground allocation with shifts in species composition (e.g., Connin et al. 1997).

Our results are consistent with previous literature. In sagebrush steppe, spring (growing-season) grazing by both sheep (Mueggler 1950, Laycock 1967, Bork et al. 1998) and cattle (Daubenmire 1940, Rickard et al. 1975, Brotherson and Brotherson 1981) reduced the abundance of perennial grasses and, in some cases, increased the abundance of shrubs. In arid PAT, Soriano (1976) found that grazing caused a decrease in the abundance of the palatable grasses and increases in the abundance of unpalatable grasses and shrubs (Soriano 1983), but the magnitude of these effects was small. In subhumid PAT, grazing more strongly reduced cover of the dominant, palatable bunchgrass and tended to increase the cover of bare ground and shrubs (León and Aguiar 1985, Bertiller 1994, Bertiller et al. 1995), and one study documented decreases in aboveground production (Bertiller and DeFossé 1990). Our data, based on one consistent methodology, provide a stronger comparison, and a rare example of a cross-continent study of grazing effects (e.g., Bock et al. 1995).

Management differences, especially the use of cattle in SGBR and sheep in PAT, confound this comparison. However, both the literature and our limited sampling in one sheep pasture demonstrated that spring grazing by cattle and sheep have similar effects on SGBR vegetation. Both animals preferentially graze perennial grasses in spring and summer, leading to a decline in grass abundance and, often, an increase in shrub abundance. Although the literature suggests that sheep are more selective and show a greater preference for forbs (Grant et al. 1985), values of the defoliation index for perennial grasses were similar in the sheep and cattle pastures. It is unlikely that our conclusions would differ had we studied SGBR grazed by sheep.

A second management difference that could confound the comparison is timing of grazing. Could continuous grazing in PAT vs. seasonal spring grazing in SGBR cause the observed difference in utilization and grazing response? With respect to utilization, continuous grazing could make detection of consumption more difficult if regrowth on individual plants is grazed repeatedly. On the other hand, considerable consumption will occur during the dormant season, when no compensation is possible, and will be easier to detect than consumption in a spring grazing regime. With respect to grazing response, because spring grazing will concentrate the impacts of defoliation during the growing season, when bunchgrasses are most sensitive, it might have stronger effects on the plant community. However, experimental results and theory suggest that continuous grazing in SGBR would increase, rather than decrease, differences with PAT. In SGBR, periods of rest during the flowering period are necessary to prevent loss of the dominant bunchgrasses (Daubenmire 1940, Blaisdell and Pechanec 1949, Caldwell et al. 1981, Ganskopp 1988). Although continuous grazing would reduce growing-season consumption, on average, it would also lead to a less uniform distribution of livestock than shorter duration, higher intensity rotations, which force animals to utilize forage more uniformly (Bailey et al. 1996). Thus, continuous grazing in SGBR would further increase impacts in sites close to water and could result in even more dramatic changes in vegetation along distance-from-water gradients.

Trends in species richness.—Grazing had weaker effects on species diversity than on species composition and production. Precipitation, not grazing intensity, was the primary determinant of plant diversity. The lack of significant grazing effects conflicts with existing conceptual models. The Milchunas et al. (1988) model predicts slight decreases in diversity with grazing in dry systems with long evolutionary histories (PAT), steeper declines in diversity in dry systems with short evolutionary histories (SGBR), and unimodal responses at sites with higher precipitation. Olff and Ritchie (1998) predict decreases in diversity for water-limited ecosystems such as sagebrush and Patagonian steppe. The responses that we observed fit neither model. At the 1-m^2 scale, a very weak unimodal trend emerged, with diversity peaking at intermediate grazing intensity. At the site scale, grazing had no effect on diversity. Stohlgren et al. (1999) found similar scale dependence in Rocky Mountain grasslands, where grazing increased richness at the 1-m^2 scale, but had no effect at the 1000-m^2 scale. Current models do not explain these scale-dependent effects of grazing on plant diversity.

Although we did not design this study to assess invasibility, some of the data on nonnative species numbers deserve attention. The number of nonnative species increased dramatically along the PAT precipitation gradients, rising from a mean of zero at the arid study area to more than 3.5 exotic species per site at the subhumid area. In SGBR, the increase was much less pronounced, suggesting much greater environmental changes along the PAT gradient, and making it an ideal system in which to study resistance to invasion. Decreases in the number of nonnatives with distance from water in both regions suggest that grazing can facilitate invasion in these systems (the relatively high number of nonnatives in long-term ungrazed SGBR sites is probably a spurious result caused by the proximity to roads of some of these sites). The effects of grazing on nonnative richness did not change with precipitation, nor did they differ between regions, in contrast to the predictions of Milchunas et al. (1988).

Prediction 2: shifts in relative abundance

Our second prediction focused on shifts in relative abundance. Given the narrower range of forage quality within the SGBR grasses, we predicted that the major shifts in relative abundance in that ecosystem would occur between the graminoid and shrub functional types, whereas in PAT the major shifts would occur within the perennial graminoid functional type, with little effect on shrubs.

We found evidence for larger shifts between the graminoid and shrub functional types in SGBR than in PAT. Contrary to our prediction, however, shifts in abundance within the graminoid functional type were greater in SGBR than in PAT. The ordinations demonstrated that some species were strong increasers and others strong decreasers at all study areas. In heavily grazed SGBR, however, less palatable species or the low-growing *Poa secunda* replaced *P. spicata* and *F. idahoensis* as the dominant, whereas the dominant PAT grasses were never displaced, even in heavily grazed sites.

One reason for these mixed results is that our comparison of changes in relative abundance is confounded by differences in utilization. Perhaps livestock do forage more selectively among the grasses in PAT than SGBR, but this difference is overwhelmed by more intense grazing pressure in SGBR. Alternatively, the magnitude of differences in palatability may not matter if small differences are sufficient to drive selective foraging. For example, one of the strong grazing decreasers in arid PAT, *P. ligularis*, has tougher leaves and equally low tissue N compared to the unpalatable *Stipa* species, but a slightly higher concentration of cell solubles (Adler 2003). This subtle difference is the only indication of higher palatability, yet it is clearly a preferred forage item. A rigorous test of either explanation would require holding grazing pressure constant in both systems.

Successes and limitations of the plant traits approach

We were successful in using differences in plant traits to predict relative differences in utilization and the magnitude of resulting changes in primary production and species composition both within and between continents. The nutritional quality and palatability of dominant grasses played a key role in determining grazing response. More generally, plant nutritional quality influences the proportion of primary production consumed as well as the growth of consumers across a wide range of ecosystems (Mattson 1980, Cebrian 1999, Cebrian and Lartigue 2004). This perspective recognizes that plant traits can influence utilization, traditionally considered an independent variable in grazing research.

We were less successful in predicting whether the greatest shifts in relative abundances would occur between or within functional types, a more specific prediction. One reason for this failure was that continental differences in utilization confounded the comparison of changes in relative abundance. But other studies have also encountered difficulties when testing species-specific predictions, especially in arid and semiarid ecosystems (Vesk and Westoby 2001, Vesk et al. 2004). The plant traits approach may be better suited to making predictions about ecosystem processes, such as consumption and the production of broad plant functional types, than community interactions, such as changes in the relative abundance of individual species.

The main limitation of the plant traits approach is its failure to explain the ultimate cause of variation within and between ecosystems. Finding that poor nutritional quality of dominant species contributes to grazing resistance in arid Patagonia begs the question, what is the origin of such poor quality? Although answering this question was not our current objective (see Adler et al. 2004), our soils results are relevant to the issue. One explanation for poor-quality leaf tissue is that millennia of heavy grazing by guanaco favored its evolution as a defense against herbivory. A second possibility is that nitrogen supply is limited by the extremely coarse soils of arid Patagonia, as indicated by N content frequently less than 0.05%. In other grassland systems, coarse soils accumulated less total N and experienced higher N mineralization rates than finer textured soils (Schimel et al. 1985*a*, *b*, Barrett and Burke 2002). The loamier soils at the subhumid Patagonian study area accumulated more organic matter and graminoid tissues at this site were richer in N. Thus, variability in soil texture may explain the continental differences in plant quality, as well as the differences within Patagonia.

Rather than treat evolutionary history of grazing and environmental factors such as soil texture as isolated variables, we should expect interactions. However, unraveling the mechanisms of plant–animal coevolution remains a considerable challenge. This case study suggests that an understanding of abiotic environments may allow predictions about whether coevolution will favor grazing avoidance or tolerance. Nitrogen limitation created by coarse-textured soils in Patagonia may have prevented the evolution of grazing-tolerant grasses such as those that form grazing lawns in the Serengeti (McNaughton 1984) or the shortgrass steppe of North America. Without a sufficient nutrient supply to permit rapid regrowth, generalized defense is a better strategy than tolerance (Coley et al. 1985, van der Meijden et al. 1988, Herms and Mattson 1992). Positive plant–animal feedbacks and extremely high animal densities need not characterize all grazing-adapted ecosystems. Where abiotic conditions are less favorable, as in arid Patagonia, a negative feedback and moderate animal densities could be the products of coevolution.

To determine the ultimate causes of variability in ecosystem response to grazing, we need to understand the evolution of plant functional traits. In contrast, useful predictions about grazing response, a goal of applied research, only require easily collected information about plant traits themselves. Our comparison of communities in sagebrush and Patagonian steppe demonstrates that plants of low forage quality can limit utilization and thus make an ecosystem more resistant to overgrazing than one dominated by undefended, palatable plants.

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LITERATURE CITED

Adler, P. B. 2003. A comparison of livestock grazing effects on sagebrush steppe, USA and Patagonian steppe, Argentina. Dissertation. Colorado State University, Fort Collins, Colorado, USA.

Adler, P. B., and S. A. Hall. 2005. The development of forage production and utilization gradients around livestock watering points. Landscape Ecology, *in press.*

Adler, P. B., D. G. Milchunas, W. K. Lauenroth, O. E. Sala, and I. C. Burke. 2004. Functional traits of graminoids in semi-arid steppes: a test of grazing histories. Journal of Applied Ecology **41**:653–663.

Allison, C. D. 1985. Factors affecting forage intake by range ruminants: a review. Journal of Range Management **38**: 305–311.

Anchorena, J., and A. M. Cingolani. 1999. Evaluación de pastizales en la Estancia Valle Huemules y propuesta de manejo. Unpublished report, Centro de Ecofisiología Vegetal, Buenos Aires, Argentina.

Andrew, M. H. 1988. Grazing impact in relation to livestock watering points. Trends in Ecology and Evolution **3**:7–11.

Bailey, D. W., J. E. Gross, E. A. Laca, L. R. Rittenhouse, M. B. Coughenour, D. M. Swift, and P. L. Sims. 1996. Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management **49**:386–400.

Bailey, H. P. 1979. Semi-arid climates: their definition and distribution. Pages 73–97 *in* A. E. Hall, G. H. Cannell, and H. W. Lawton, editors. Agriculture in semi-arid environments. Ecological Studies 34. Springer-Verlag, New York, New York, USA.

Barrett, J. E., and I. C. Burke. 2002. Nitrogen retention in semiarid ecosystems across a soil organic matter gradient. Ecological Applications **12**:878–890.

Beltrán, A. 1997. Caracterización microclimática del distrito occidental de la estepa Patagónica. Thesis. University of Buenos Aires, Buenos Aires, Argentina.

Bertiller, M. B. 1994. Modelos ecológicos alternativas de la dinámica de la vegetatción en ecosistemas de pastizales: Un caso de estudio en la Patagonia. Revista Argentina de Producción Animal **14**:15–23.

Bertiller, M. B., and G. E. DeFossé. 1990. Grazing and plant growth interactions in a semiarid *Festuca pallescens* grassland (Patagonia). Journal of Range Management **43**:300–303.

Bertiller, M. B., N. O. Elissalde, C. M. Rostagno, and G. E. DeFossé. 1995. Environmental patterns and plant distribution along a precipitation gradient in western Patagonia. Journal of Arid Environments **29**:85–97.

Blaisdell, J. P., and J. F. Pechanec. 1949. Effects of herbage removal at various dates on vigor of bluebunch wheatgrass and arrowleaf balsamroot. Ecology **30**:298–305.

Bock, J. H., C. L. Jolls, and A. C. Lewis. 1995. The effects of grazing on alpine vegetation: a comparison of the central Caucuses, Republic of Georgia, with the Colorado Rocky Mountains, USA. Arctic and Alpine Research **27**:130–136.

Bork, E. W., N. E. West, and J. W. Walker. 1998. Cover components on long-term seasonal sheep grazing treatments in three-tip sagebrush steppe. Journal of Range Management **51**:293–300.

Borrelli, P. 2001. Producción animal sobre pastizales naturales. Pages 129–159 *in* P. Borrelli and G. Oliva, editors. Ganadería Sustentable en la Patagonia Austral. INTA (Instituto Nacional de Technologí Agropecuaria), Centro Regional Patagonian Sur, Buenos Aires, Argentina.

Brotherson, J. D., and W. T. Brotherson. 1981. Grazing impacts on the sagebrush communities of central Utah. Great Basin Naturalist **41**:335–340.

Burke, I. C., W. K. Lauenroth, and D. G. Milchunas. 1997. Biogeochemistry of managed grasslands in Central North America. Pages 85–102 *in* E. A. Paul, E. T. Elliot, K. Paustian, and C. V. Cole, editors. Soil organic matter in temperate agroecosystems. CRC Press, Boca Raton, Florida, USA.

Butler, B. R. 1978. Bison hunting in the desert west before 1800: the paleo-ecological potential and the archaeological reality. Plains Anthropologist **23**:106–112.

Caldwell, M. M., J. H. Richards, D. A. Johnson, R. S. Nowak, and R. S. Dzurec. 1981. Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. Oecologia **50**:14–24.

Cebrian, J. 1999. Patterns in the fate of production in plant communities. American Naturalist **154**:449–468.

Cebrian, J., and J. Lartigue. 2004. Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. Ecological Monographs **74**:237–259.

Coley, P. D., J. P. Bryant, and F. S. Chapin, III. 1985. Resource availability and plant–herbivore defense. Science **230**:895–899.

Connin, S. L., R. A. Virginia, and C. P. Chamberlain. 1997. Carbon isotopes reveal soil organic matter dynamics following arid land shrub expansion. Oecologia **110**:374–386.

Correa, M. V. 1969–1999. Flora Patagónica. INTA, Buenos Aires, Argentina.

Coughenour, M. B. 1991. Spatial components of plant–herbivore interactions in pastoral, ranching, and native ungulate ecosystems. Journal of Range Management **44**:530–542.

Daly, C., R. P. Neilson, and D. L. Phillips. 1994. A statistical-topographic model for mapping climatological precipitation over mountanious terrain. Journal of Applied Meteorology **33**:140–158.

Daubenmire, R. F. 1940. Plant succession due to overgrazing in the *Agropyron* bunchgrass prairie of southeastern Washington. Ecology **21**:55–64.

Daubenmire, R. 1970. Steppe vegetation of Washington. Technical Bulletin 62. Washington Agricultural Station, College of Agriculture, Washington State University, Pullman, Washington, USA.

Díaz, S., A. Acosta, and M. Cabido. 1992. Morphological analysis of herbaceous communities under different grazing regimes. Journal of Vegetation Science **3**:689–696.

Díaz, S., A. Acosta, and M. Cabido. 1994. Community structure in montane grasslands of central Argentina in relation to land use. Journal of Vegetation Science **5**:483–488.

Díaz, S., I. Noy-Meir, and M. Cabido. 2001. Can grazing response of herbaceous plants be predicted from simple vegetative traits? Journal of Applied Ecology **38**:497–508.

Fernández, R. J. 1986. Papel del pastoreo ovino en la dinamica poblacional de dos arbustos en la estepa Patagónica. Thesis. University of Buenos Aires, Buenos Aires, Argentina.

Fernández, R. J., O. E. Sala, and R. A. Golluscio. 1991. Woody and herbaceous aboveground production of a Patagonian steppe. Journal of Range Management **44**:434–436.

Franklin, W. L. 1981. Biology, ecology, and relationship to man of the South American camelids. Pages 457–489 *in* M. A. Mars and H. H. Genoways, editors. Mammalian biology in South America. Special Publication Series, University of Pittsburgh, Pittsburgh, Pennsylvania, USA.

Ganskopp, D. 1988. Defoliation of Thurber needlegrass: herbage and root responses. Journal of Range Management **41**:472–476.

Golluscio, R. A., J. M. Paruelo, J. L. Mercau, and V. A. Deregibus. 1998. Urea supplementation effects on the utilization of low-quality forage and lamb production in Patagonian rangelands. Grass and Forage Science **53**:47–56.

Grant, S. E., D. E. Suckling, H. K. Smith, L. Torvell, T. D. A. Forbes, and J. Hodgson. 1985. Comparative studies of diet selection by sheep and cattle: the hill grasslands. Journal of Ecology **73**:987–1004.

Herms, D. A., and W. J. Mattson. 1992. The dilemma of plants: to grow or defend. Quarterly Review of Biology **67**:283–335.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest: an illustrated manual. University of Washington Press, Seattle, Washington, USA.

Küchler, A. W. 1964. Potential natural vegetation of the conterminous United States. Special Publication Number 36. American Geographical Society, New York, New York, USA.

Lange, R. T. 1969. The piosphere: sheep track and dung patterns. Journal of Range Management **22**:396–400.

Lauenroth, W. K. 1998. Guanacos, spiny shrubs and the evolutionary history of grazing in the Patagonian steppe. Ecología Austral **8**:211–216.

Laycock, W. A. 1967. How heavy grazing and protection affect sagebrush–grass ranges. Journal of Range Management **20**:206–213.

León, R. C. J., and M. R. Aguiar. 1985. El deterio por uso pasturil en estepas herbáceas patagónicas. Phytocoenologia **13**:181–196.

León, R. J. C., D. Bran, M. Collantes, J. M. Paruelo, and A. Soriano. 1998. Grandes unidades de vegetación de la Patagonia extra andina. Ecología Austral **8**:125–144.

Lyman, R. L., and S. Wolverton. 2002. The late prehistoric–early historic game sink in the northwestern United States. Conservation Biology **16**:73–85.

Mack, R. N., and J. N. Thompson. 1982. Evolution in steppe with few large, hooved mammals. American Naturalist **119**: 757–73.

Mattson, W. J., Jr. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics **11**:119–161.

McIntyre, S., S. Lavorel, J. Landsberg, and T. D. A. Forbes. 1999. Disturbance response in vegetation towards a global perspective on functional traits. Journal of Vegetation Science **10**:621–630.

McNaughton, S. J. 1984. Grazing lawns: animals in herds, plant form, and coevolution. American Naturalist **124**:863–886.

Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs **63**:327–366.

Milchunas, D. G., O. E. Sala, and W. K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. American Naturalist **132**:87–106.

Miller, R. F., T. J. Svejcar, and N. E. West. 1994. Implications of livestock grazing in the Intermountain Sagebrush Region: plant composition. Pages 101–146 *in* M. Vavra, W. A. Laycock, and R. D. Pieper, editors. Ecological implications of livestock herbivory in the West. Society for Range Management, Denver, Colorado, USA.

Mueggler, W. F. 1950. Effects of spring and fall grazing by sheep on vegetation of the Upper Snake River Plains. Journal of Range Management **3**:308–315.

Nash, M. S., W. G. Whitford, A. G. de Soyza, J. W. Van Zee, and K. M. Havstad. 1999. Livestock activity and Chihuahuan Desert annual-plant communities: boundary analysis of disturbance gradients. Ecological Applications **9**:814–823.

Oesterheld, M., and S. J. McNaughton. 2000. Herbivory in terrestrial ecosystems. Pages 151–157 *in* O. E. Sala, R. B. Jackson, H. A. Mooney, and R. W. Howarth, editors. Methods in ecosystem science. Springer-Verlag, New York, New York, USA.

Olff, H., and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. Trends in Ecology and Evolution **13**:261–265.

Paruelo, J. M., E. G. Jobbagy, O. E. Sala, W. K. Lauenroth, and I. C. Burke. 1998. Functional and structural convergence of temperate grassland and shrubland ecosystems. Ecological Applications **8**:194–206.

Paruelo, J. M., W. K. Lauenroth, H. E. Epstein, I. C. Burke, and M. R. Aguiar. 1995. Regional climatic similarities in the temperate zones of North and South America. Journal of Biogeography **22**:915–925.

Paruelo, J. M., and O. E. Sala. 1992*a*. El impacto de la desertificación sobre la capacidad de carga de las estepas Patagónicas: sus consequencias económicas. Unpublished report, INTA-GTZ (Instituto Nacional de Tecnología Agropecuaria-Gesellscheft für Technische Zusammenarbeit), Buenos Aires, Argentina.

Paruelo, J. M., and O. E. Sala. 1992*b*. El impacto de la desertificación sobre la capacidad de carga de las estepas Patagónicas: sus consequencias económicas. II Congreso Latinoamericano de Ecología, Caxambú, Brasil.

Pickup, G., G. N. Bastin, and V. H. Chewings. 1998. Identifying trends in land degradation in non-equilibrium rangelands. Journal of Applied Ecology **35**:365–377.

Redfern, J. V., R. Grant, H. Biggs, and W. M. Getz. 2003. Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. Ecology **84**:2092–2107.

Rickard, W. H., D. W. Uresk, and J. F. Cline. 1975. Impact of cattle grazing on three perennial bunchgrasses in south-central Washington. Journal of Range Management **28**: 108–112.

SAS Institute. 1999. SAS 8.2. Proc. Mixed SAS Institute, Cary, North Carolina, USA.

Schimel, D. S., D. C. Coleman, and K. A. Horton. 1985*a*. Soil organic matter dynamics in paired rangeland and cropland toposequences in North Dakota. Geoderma **36**:201–214.

Schimel, D., M. A. Stillwell, and R. G. Woodmansee. 1985*b*. Biogeochemistry of C, N, and P in a soil catena of the shortgrass steppe. Ecology **66**:276–282.

Solbrig, O. T. 1973. The origin and floristic affinities of the South American temperate desert and semidesert regions. Pages 7–49 *in* D. W. Goodall, editor. Evolution of desert biota. University of Texas Press, Austin, Texas, USA.

Somlo, R., G. Bonvissuto, N. Bonino, A. Pelliza Sbrilller, and E. Moricz. 1992. Diet relationships among sheep and sympatric herbivores in NW Patagonia, Argentina. World Sheep and Wool Congress, 6–12 August, Buenos Aires, Argentina.

Soriano, A. 1976. Ecología del pastizal de coirón amrgo (*Stipa* spp.) del sudoeste de Chubut. Academia Nacional de Agronomia y Veterinaria, Buenos Aires, Argentina.

Soriano, A. 1983. Deserts and semi-deserts of Patagonia. Pages 423–460 *in* N. E. West, editor. Temperate deserts and semi-deserts. Ecosystems of the World 5. Elsevier Scientific, New York, New York, USA.

Soriano, A., and J. M. Paruelo. 1990. El Pastoreo Ovino: principios ecológicos para el manejo de los campos. Ciencia Hoy **2**:44–53.

Stohlgren, T. J., L. D. Schell, and B. Vanden Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecological Applications **9**:45–64.

Swift, L. W., Jr. 1976. Algorithm for solar radiation on mountain slopes. Water Resources Research **12**:108–112.

ter Braak, C. J. F., and P. Smilauer. 1999. CANOCO for Windows. Version 4.02. Centre for Biometry Wageningen, CPRO-DLO (Centre for Plant Breeding and Reproduction Research), Wageningen, The Netherlands.

Turner, M. D. 1998. Long-term effects of daily grazing orbits on nutrient availability in Sahelian West Africa: I. Gradients in the chemical composition of rangeland soils and vegetation. Journal of Biogeography **25**:669–682.

Valentine, K. A. 1947. Distance from water as a factor in grazing capacity of rangeland. Journal of Forestry **45**:749–754.

van der Meijden, E., M. Wijn, and H. J. Verkaar. 1988. Defence and regrowth, alternative plant strategies in the struggle against herbivores. Oikos **51**:355–363.

Vesk, P. A., M. R. Leishman, and M. Westoby. 2004. Simple traits do not predict grazing response in Australian dry shrublands and woodlands. Journal of Applied Ecology **41**: 22–31.

Vesk, P. A., and M. Westoby. 2001. Predicting plant species' responses to grazing. Journal of Applied Ecology **38**:897–909.

Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: some leading dimensions of variation between species. Annual Review of Ecology and Systematics **33**:125–159.

Wolfe, J. A. 1969. Neogene floristic and vegetational history of the Pacific Northwest. Madroño **20**:83–110.

APPENDIX A

Detailed methods for primary production and soil sampling are available in ESA's Ecological Data Archive: *Ecological Archives* A015-019-A1.

APPENDIX B

Statistical tables for single-year mixed-effects models are available in ESA's Ecological Data Archive: *Ecological Archives* A015-019-A2.

APPENDIX C

Statistical tables for repeated-measures mixed-effects models are available in ESA's Ecological Data Archive: *Ecological Archives* A015-019-A3.

APPENDIX D

Table D1 (distance-from-water classes), Fig. D1 (consumption vs. distance from water), Fig. D2 (forage utilization vs. distance from water), Fig. D3 (perennial grass basal cover vs. distance from water at six study areas differing in aridity), Fig. D4 (repeated-measures test results for shrub production vs. distance from water), Fig. D5 (nonnative species per site vs. distance from water and precipitation), and Fig. D6 (soil concentration of C and N at six study areas differing in aridity) are available in ESA's Electronic Data Archive: *Ecological Archives* A015-019-A4.