DISSERTATION

A COMPARISON OF LIVESTOCK GRAZING EFFECTS ON SAGEBRUSH STEPPE, USA, AND PATAGONIAN STEPPE, ARGENTINA

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY PETER B. ADLER ENTITLED "A COMPARISON OF LIVESTOCK GRAZING EFFECTS ON SAGEBRUSH STEPPE, USA, AND PATAGONIAN STEPPE, ARGENTINA," BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

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Grazing by domestic livestock has dramatic effects on vegetation in some ecosystems but only subtle effects in others. Ecosystem response to grazing is determined by the frequency and degree of plant functional traits related to grazing tolerance and avoidance, which, in turn, are influenced by both precipitation and evolutionary history of grazing. To test the power of evolutionary history to explain variability in the effects of grazing on vegetation, I compared vegetation response to grazing in the sagebrush steppe of North American and the Patagonian steppe of South American. These regions have very similar precipitation regimes, but evidence suggests a shorter evolutionary history of grazing in sagebrush compared to Patagonian steppe. Therefore, I expected the Patagonian steppe to be more grazing resistant than sagebrush steppe.

My comparison of plant traits showed that sagebrush steppe grasses have significantly higher forage quality than Patagonian grasses, based on measurements of tissue nitrogen and fiber content. Sagebrush steppe grasses also tend to be taller than Patagonian grasses. These characteristics may explain why consumption and utilization by livestock are higher in sagebrush steppe. As a consequence of more intense grazing, decreases in perennial grass production and cover and increases in shrub abundance across distance from water gradients, proxies for historical grazing impacts, were more dramatic in sagebrush than Patagonian steppe. The grazing resistance of Patagonian steppe, therefore, appears to depend on the low forage quality of the dominant grasses.

Evolutionary history of grazing offers one possible explanation for lower forage quality in Patagonian grasses, since it may have evolved as a defense against grazing. However, differences in abiotic factors lead to an alternative explanation: Patagonia's more extensive arid zone might have favored the evolution of xerophytic traits, and potential nitrogen limitation created by sandy soils could explain the low N content of the dominant grasses. Consistent with this hypothesis, total soil N was much lower in arid Patagonia, where soils are extremely sandy, than in sagebrush sites with similar levels of aboveground production. Understanding the evolution of plant traits will require unraveling the interacting effects of abiotic factors and evolutionary history of grazing.

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CHAPTER 1: INTRODUCTION

Arid and semiarid climates, supporting shrubland and grassland ecosystems, cover 32% of the Earth's land surface (Bailey 1996). A major anthropogenic factor affecting native vegetation in these regions is domestic livestock grazing (Milchunas and Lauenroth 1993). Though grazing is common to many ecosystems, its effects on vegetation and soils are extremely variable. In some ecosystems, such as the shortgrass steppe of eastern Colorado, grazing has only subtle effects on plant communities (Milchunas et al. 1989). In fact, the exclusion of grazing may lead to undesirable changes such as an increase in the abundance of non-native species (Milchunas et al. 1992). Livestock grazing in other ecosystems, such as the sagebrush steppe of the Intermountain west, has been associated with dramatic decreases in forage production, increases in soil erosion, and widespread plant invasions causing large economic losses (Daubenmire 1970, Mack 1981, Miller et al. 1994).

Given the global extent of shrubland and grassland ecosystems influenced by livestock grazing and its potentially damaging impacts, ecologists have devoted considerable effort to understanding why grazing has such different effects in different locations. Current research has focused on testing the hypothesis that the effects of grazing are determined by the functional traits of plant species (Díaz et al. 1992, 2001, McIntyre et al. 1999, Bullock et al. 2001, McIntyre and Lavorel 2001). This hypothesis predicts that grazing impacts will be smaller in systems where traits conferring resistance to grazing are well developed and common among plant species than in systems where such traits are poorly developed or rare.

Although plant traits may provide the proximate cause for differences in grazing effects in different ecosystems, they do not provide an ultimate cause. Identifying the ultimate cause requires understanding the selection pressures that determine plant functional traits. One factor that clearly influences the selection of plant traits in evolutionary and ecological time is climate, and previous research has identified links between climate, precipitation in particular, and the effect of grazing on plant species composition (Milchunas et al. 1988, Olff and Ritchie 1998). Because plant functional traits associated with drought resistance, such as short stature and rapid leaf turnover, also tend to provide resistance to grazing (Coughenour 1985), we expect the magnitude of the effect of grazing on vegetation to decrease as precipitation decreases (Milchunas et al. 1988). A second factor determining whether plants evolve grazing resistant traits is the evolutionary history of grazing, meaning the intensity of selection pressures imposed on plants by grazers over an ecologically relevant timescale (Larson 1940, Stebbins 1981, Mack and Thompson 1982, Milchunas et al. 1988). The evolutionary history of grazing concept predicts that systems that have been intensively grazed by large herds of wild ungulates will be resistant to grazing. According to this model, the reason that the shortgrass steppe of North America is so resistant to livestock grazing is its history of grazing by large herds of bison, which forced plants to evolve appropriate adaptations (Milchunas et al. 1989).

While evolutionary history of grazing is frequently offered as a *post hoc* explanation for the observed sensitivity or resistance to grazing of a particular ecosystem, I am aware of only one rigorous test of the concept's explanatory power. Milchunas and Lauenroth (1993) reviewed grazing studies from a global range of environments and showed that independent, subjective ratings of each site's evolutionary history of grazing explained a significant amount of variation in vegetation responses. For my dissertation research, intended to test the explanatory power of the evolutionary history of grazing concept, I explored an alternative to this meta-analysis approach that relied on a comparison of climatically analogous ecosystems with independent evolutionary histories of grazing. In the 19th century, continental comparisons led to recognition of the relationship between climate and vegetation structure, one of the first successful generalizations in ecology (Grisebach 1845, von Humboldt 1849). Modern studies of similarity between Mediterranean (Cody and Mooney 1978) and hot desert ecosystems (Orians and Solbrig 1977) on different continents formalized this relationship as the convergence hypothesis, which in its simplest form states that the degree of biotic similarity is a function of the degree of abiotic similarity. I used the convergence hypothesis to test whether differences in evolutionary history can explain differences in the effect of grazing on vegetation. In order to do this, I searched for a continental comparison that would hold climate constant, so that differences in plant traits would be a function of differences in biological selection pressures such as grazing.

The sagebrush steppe of North America's Intermountain west and the Patagonian steppe of southern Argentina allow this comparison. These two ecosystems, occupying rain shadow deserts east of the Cascades and Andes, have similar geology as well as historical and contemporary climates (Solbrig 1973, Daubenmire 1975, Paruelo et al. 1995). According to the convergence hypothesis, this similarity in abiotic factors should lead to convergence in plant functional traits. Available evidence, however, suggests that these two ecosystems have different evolutionary histories of grazing. While the sagebrush steppe had few ungulate grazers during the Holocene (Mack and Thompson 1982, Lyman and Wolverton 2002), high densities of guanaco grazed at least some parts of the Patagonian steppe into the mid-20th century (Franklin 1981, Lauenroth 1998).

The central hypothesis of my dissertation is that evolutionary history of grazing is an important determinant of the effect of livestock grazing on plant communities. This hypothesis leads to the prediction that the more intense evolutionary history of grazing in Patagonia should have produced grazing resistance at the plant trait level and, in turn, at the plant community level relative to the sagebrush steppe. I evaluated this prediction by attempting to answer three main research questions and a fourth question relating to methodology:

First, how similar are the driving abiotic factors in sagebrush and Patagonian steppe? No two ecosystems will have perfectly equivalent environments, and subtle environmental differences may have large implications for ecological processes, especially at the level of consumers (Orians and Solbrig 1977, Cody and Mooney 1978). These abiotic constrasts must be considered alongside evolutionary history as alternative explanations for differences in ecological structure and function. In **Chapter 2** I explore the similarities and differences of abiotic factors in sagebrush and Patagonian steppe, and attempt to identify those with the most important ecological implications.

Second, do differences in functional traits of common graminoids from sagebrush and Patagonian steppe provide evidence for a longer evolutionary history of grazing in Patagonia? Do these differences suggest mechanisms for greater resistance to contemporary livestock grazing? In **Chapter 3** I compare plant traits related to tolerance and avoidance of grazing among the primary forage species of both ecosystems. This comparison serves to provide evidence for differences in the evolutionary history of grazing, since the plant traits are the legacies of historical selection pressures, and also to indicate how current domestic livestock grazing will impact these ecosystems, since a flora rich in adaptations to grazing should be more resistant to changes caused by grazing.

Third, are differences in the effect of grazing on these ecosystems consistent with the prediction that, because of its longer evolutionary history of grazing, the Patagonian steppe is more resistant to grazing than the sagebrush steppe? To answer this question, I sampled consumption and utilization by livestock, primary production, plant species composition, and soil fertility across gradients of grazing pressure in arid, semarid, and subhumid study areas in each ecosystem. In **Chapter 4**, I report on the results of these field studies and evaluate their support for the prediction of stronger grazing resistance in Patagonia.

Fourth, since the field studies in Chapter 4 provided evidence of unexpected spatial patterns in grazing intensity, I built a series of foraging simulation models to understand how the distribution of grazing changes as vegetation patterns are altered by grazing. I also used these models, described in **Appendix I**, to identify the foraging behaviors that generate the most realistic patterns in the simulated distribution of vegetation and grazing pressure.

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CHAPTER 2: CONDITIONS FOR CONVERGENCE: COMPARISON OF ABIOTIC FACTORS IN SAGEBRUSH STEPPE, USA AND PATAGONIAN STEPPE, ARGENTINA

ABSTRACT

The sagebrush steppe of North America and the Patagonian steppe of South America offer an ideal comparison for the study of convergent evolution because of their closely matching geology and macroclimate. The vulnerability of these ecosystems to impacts of domestic livestock grazing and biological invasions makes this comparison of special interest. However, because the degree of convergence will depend on the degree of abiotic similarity, it is important to understand even subtle differences in abiotic factors. I used climate and soils data, a soil water model, and satellite data to compare these two ecosystems' historic and contemporary abiotic environments, as well as dynamics of evapotranspiration and normalized difference vegetation index (NDVI). Historic and contemporary similarity in patterns of precipitation, the driving abiotic variable in these ecosystems, creates conditions for strong ecological convergence. Nevertheless, Patagonia's larger arid region may select more intensely for xerophytic plant traits. Analyses based on a soil water model and NDVI suggest that Patagonia's narrower thermal amplitude and sandier soils interact to produce a longer growing season compared to sagebrush steppe. The difference in soil texture also suggests a greater

potential for nitrogen limitation in Patagonian steppe. These differences complicate but should not preclude this interesting continental comparison.

INTRODUCTION

The striking similarity among ecosystems with similar climatic regimes generated some of the earliest successful generalizations in ecology (Grisebach 1845, von Humboldt 1849). This early work in biogeography and systematic botany led to modern comparative ecological studies designed to test the importance of convergent evolution (Orians and Solbrig 1977, Cody and Mooney 1978, West 1983). The simplest statement of the convergence hypothesis is that similarity in ecosystem structure is a function of similarity in abiotic factors. In warm deserts (Orians and Solbrig 1977), temperate deserts (West 1983), and Mediterranean systems (Cody and Mooney 1978), similarity among primary producers provided strong support for the hypothesis, but contrasts at the level of consumers suggested that convergence weakens as ecological interactions become important relative to physical factors.

While the comparative ecosystem approach has been used primarily in basic research aimed at understanding controls on ecosystem structure and function, it also lends itself to applied questions. For example, a conceptual model currently used to predict the impacts of livestock grazing (Milchunas et al. 1988) includes both precipitation and evolutionary history as independent variables. Rigorous tests of this model would require comparisons of areas with independent evolutionary histories--continental comparisons--along with careful consideration of potentially confounding differences in their climatic regimes. Efforts to understand why some ecosystems are more resistant to biological invasions than others have also taken advantage of global comparisons (Lonsdale 1999), but here too abiotic differences may confound apparent generalizations. Therefore, although continental comparisons have the potential to test ecological theory, we must be careful to account for environmental covariates.

The sagebrush steppe of North America and the Patagonian steppe of southern Argentina provide an ideal continental comparison because of their closely matching geological history (Axelrod 1979) and climate (West 1983, Paruelo et al. 1995). Despite recognition of this macroscale similarity, the potential for biological comparison remains unexploited, the exception being studies of granivory rates (Folgarait et al. 1998). Furthermore, this comparison presents an opportunity to test our understanding of applied ecological problems. Domestic livestock grazing is a dominant land-use in both regions (Soriano 1983, Miller et al. 1994), and biological invasions are a critical concern in the sagebrush steppe (Mack 1981) but, curiously, not in Patagonian steppe.

As I argued above, any comparison of these ecosystems should be preceded by a careful analysis of their environmental similarities and differences. Differences in individual climate and soil variables can be easily calculated, but determining their collective ecological importance requires a method for integration. In arid and semiarid ecosystems, water availability is the driving abiotic variable, responsible for dynamics of primary and secondary production (Noy Meir 1973, Sala et al. 1992). Therefore, we should evaluate the influence of differences in climate or soils on water availability, which we can do with existing simulation models (Parton 1978, Paruelo and Sala 1995). We can use primary production, which depends strongly on water availability in water-limited ecosystems (Sala et al. 1988), as an additional integrating variable (McNaughton et al. 1989). Direct measures of primary production are limited, but satellite derived measures of vegetation activity, a proxy for primary productivity, provide appropriate data related to phenology and productivity at regional scales (Paruelo et al. 1998).

My objective was to investigate the degree of similarity in the abiotic factors of the sagebrush steppe and Patagonian steppe, a prerequisite to future studies of ecological convergence. My analysis contained two parts. First, I identified similarities and differences in historical and present climate as well as geology and soils. Second, using a soil water model and a satellite derived vegetation index, I evaluated which of these contrasts could have the most important ecological implications.

METHODS

Study areas

Both the Intermountain west of North America and southern South America east of the Andes contain a heterogeneous mix of arid and semiarid ecosystems. For the purposes of comparison, I grouped the vegetation types within each region into three general classes: areas dominated by bunchgrasses with a minor shrub component, areas in which bunchgrasses and shrubs are co-dominants, and shrublands in which grasses have low relative abundance. In the North American study region, the bunchgrass-dominated areas correspond to Küchler's (1964) "Fescue/Wheatgrass" and "Wheatgrass/Bluegrass" vegetation types, and the bunchgrass-shrub areas correspond to Küchler's "Sagebrush-steppe." I refer to the combined area of both these vegetation types as sagebrush steppe, and specify grass or grass-shrub areas to identify the specific vegetation type within the region. This vegetation occurs primarily in the Columbia Plateau of eastern Washington, Oregon, and southern Idaho, but includes areas at the northern extreme of the Great Basin, in Nevada, and portions of western Wyoming as well (Fig. 2.1). The South American study area includes the bunchgrass dominated "Subandean District" (Soriano 1983, León et al. 1998) and the bunchgrass and shrub dominated "Occidental District," located primarily in the southern Argentine provinces of Neuquén, Río Negro, Chubut, and Santa Cruz (Fig. 2.1). I refer to these two vegetation types collectively as Patagonian steppe.

I did not include the shrub-dominated areas of each ecosystem in the comparison because the "Great Basin sagebrush" vegetation type of North America (Küchler 1964) (Fig. 2.1), occurring at latitudes below 40°N, tends to be much hotter than the cool, arid shrublands of Patagonia's "Central District" (León et al. 1998), which occur at latitudes greater than 40°S.

Climate data

To characterize regional precipitation in the sagebrush steppe, I used mean annual values from PRISM, a model that interpolates between data points using a digital elevation model to capture orographic effects (Daly et al. 1994). For Patagonia, I combined data from the U.S. National Climatic Data Center and Argentina's Instituto Nacional de Tecnología Agropecuaria (INTA), and then interpolated these data using a distance weighting method (ArcView 3.2).

To further compare seasonal climatic trends in the sagebrush steppe and Patagonia, and to provide climatic inputs for soil water modeling, I selected one site from each region with both meterological and corresponding ecological data: the Arid Lands Ecology Reserve (ALE) on the U.S. Department of Energy's Hanford Reservation in central Washington state, and Río Mayo (RM), a field experiment station administered by INTA in southwestern Chubut province. Each of these sites offers long term daily data for precipitation, wind, and mean and maximum temperature (Hoitink et al. 1999, Beltrán 1997).

Soils data

I used the U.S. Department of Agriculture, Natural Resource Conservation Service's State Soil Geographic database (STATSGO) for information on soil taxonomy and soil texture in sagebrush steppe. The soil texture data were based on surface horizons, and I combined more specific classifications into second order groups ("cobbly sandy loam" becomes "sandy loam"). Equivalent information for Patagonia was obtained from the Atlas de Suelos de la República Argentina (Moscatelli 1990).

Evapotranspiration

I evaluated the effect of regional differences in soil and climate on evapotranspiration using the "Soilwat" simulation model parameterized for the shortgrass steppe of eastern Colorado (Parton 1978). Soilwat requires three classes of input data: 1) timing and magnitude of vegetation biomass, 2) weather data including daily precipitation and temperature, and mean monthly wind speed and radiation, and 3) soil variables for each specified soil layer. Because I was primarily interested in comparing the effects of abiotic differences, I held vegetation constant in all simulations by creating one set of vegetation parameters based on data from both RM (Soriano 1983) and ALE (Rickard et al. 1988). Since I had twelve complete but not successive years of daily weather data for RM, I matched each RM weather year with an ALE weather year having similar annual precipitation, producing a dataset of twelve independent weather years for each region. By pairing weather years, the emphasis of the analysis shifts from differences in mean precipitation to differences in the timing of precipitation. Mean monthly wind velocity was available at the 2 m elevation for RM and 10 m for ALE. I transformed the ALE data to 2 m based on a standard logarithmic elevation-wind speed relationship (R. Pielke, *pers. comm.*). I used mean monthly radiation data from ALE for all simulation runs. Since soils at both the RM and ALE sites are vertically quite homogeneous (Paruelo and Sala 1995, Rickard 1988), I based my choice of soil layers on the depth zonation of plant roots (Paruelo and Sala 1995). A. Cesa provided soil texture information for RM. For ALE, I sampled soil from the site where vegetation measurements had been made and determined texture using the hydrometer method.

In the simulation runs, I held vegetation constant but manipulated ALE and RM values of three "variables:" 1) daily precipitation and temperature, 2) mean monthly wind speed, and 3) soils. Each simulation run consisted of twelve independent climate years (fall through summer), with soil water values reset at the start of each climate year. I then compared the transpiration, evaporation, and change in soil water storage averaged across each set of twelve one-year simulations. Initializing soils of different texture at equal percentages of wilting point leads to differences in modeled evapotranspiration. Therefore, I chose soil water initialization values so that the mean change in soil water storage, over all twelve years, would be close to zero when running ALE weather and wind on ALE soils, and likewise, RM weather and wind on RM soils. I accomplished this by initializing each soil layer at 80% of wilting point for ALE soils and 75% for RM soils at the start of each climate year. These initialization values were then used in all runs on the corresponding soil type, regardless of substitutions in weather and wind data.

NDVI

Satellite-derived normalized difference vegetation index (NDVI) provides a measure of radiation interception by vegetation (Box, Holben and Kalb. 1989). Thus, NDVI is a surrogate for vegetation activity integrating across climate, soils, and vegetation. Since growing season was a constant independent variable in the soil water model analysis, the model results were not useful for comparing seasonality in sagebrush and Patagonian steppe. Regional NDVI data, in contrast, describe the timing and intensity of the growing season in each ecosystem.

I used NDVI images provided by NOAA's advanced very high resolution radiometer (AVHRR). For South America, I used images from the only available high quality data source, the Pathfinder AVHRR Land program (PAL) with a resolution of 8 km (Agbu and James 1994, James and Kalluri 1994). For North America, I used the USGS Local Area Coverages with a resolution of 1 km (Eidenshink and Faundeen 1994). I decided that the high degree of topographic and land-use heterogeneity in the sagebrush steppe required this finer resolution data, even though the difference in data sources would confound between-region comparisons of absolute NDVI values. NDVI was calculated as (Refl 2 – Refl 1)/(Refl 2 + Refl 1), where Refl 1 is the reflectance of channel 1 (0.58-0.68 μm) and Refl 2 is the reflectance of channel 2 (0.725-1.1 μm). The period of analysis spans 1991-1999 for North America, and 1981-1999 for South America. I reprocessed data from each source to obtain monthly composites for each pixel. Because of problems with satellite operation, 1994 was excluded from both time series.

I selected all pixels within the study area in each region (Fig. 2.1). I filtered out pixels dominated by urban and agricultural land uses in North American using the USGS National Land Cover Database. Such filtering was unnecessary in Patagonia, where agricultural and urban areas are extremely rare. To remove pixels dominated by forests and wet meadows in both regions, I then filtered all pixels having mean NDVI values in the peak growing season (December in Patagonia and June in sagebrush steppe) greater than 0.6 (Paruelo et al. 1999). Finally, to produce mean seasonal NDVI curves, I averaged the values of all pixels within each vegetation type (grass and grass-shrub) by month. I do not show results from the three winter months due to inconsistent temporal coverage.

RESULTS

Climate

Given the importance of past climates in shaping contemporary plant communities, I first considered the historical climate of each region. Palynological analysis provides the evidence for these reconstructions; Daubenmire (1975) is the source for most of the following discussion of the sagebrush steppe, with a focus on the Columbia Plateau of eastern Oregon and Washington. During the Paleocene and Eocene (up to 57 Mya), this area was wet and frost free, dominated by forests composed of both tropical and temperate tree species. Continental cooling during the Oligocene (37-24 Mya) forced a southward retreat of tropical plants. By the start of the Pliocene (5-2 Mya), the Cascade Mountains of Oregon and Washington had reached an elevation of 1000 masl (Daubenmire 1975, Wolfe 1969), but by the mid-Pliocene, these volcanically active mountains were high enough to create a large rain shadow and summer drought (Wolfe 1969). Increasing aridity caused the replacement of mesophytic with xerophytic species. This floristic transition was complete by the Pleistocene, so that the flora during this period was not significantly different from the modern flora. Pleistocene glaciations resulted in range shifts, but not large changes in overall species composition (Daubenmire 1975, Nowak et al 1994). The alternation of cool, wet periods and warmer, drier periods, continued through the Holocene, producing additional range shifts but not species replacements (Daubenmire 1975, Jensen et al. 1997, Nowak et al. 1994, Grayson 2000).

The climate history of Patagonia followed a similar chronology. Warm and wet conditions, as evidenced by tremendous coal deposits, persisted throughout the first half of the Tertiary (beginning 66 Mya) (Soriano 1983). Andean uplift began to the north during the Eocene, but did not begin in Patagonia until the mid-Miocene (Solbrig 1973). Uplift was complete by the end of the Pliocene. Extensive grasslands and some semi-deserts appeared in the lee of the Andes by the end of the Miocene, with more extensive semi-deserts by the end of the Pliocene (Solbrig 1973). Pleistocene glaciations did not cover extra-Andean Patagonia (Soriano, 1983). As in the sagebrush steppe, alternating warm-dry and cool-moist periods throughout the Quaternary resulted in plant range shifts, but semi-arid steppe, established during the Pleistocene (Solbrig 1973), dominated throughout (Soriano 1983).

The contemporary climate in both sagebrush and Patagonian steppe is characterized above all by dramatic precipitation gradients (Fig. 2.2). Both regions, at latitudes of roughly 40-50°, are dominated by maritime polar air masses that create cool, moist winters and dry summers. The Cascades and Andes, located on the west coast of their respective continents, cast orographically induced rain shadows across the lowlands to their east. In the sagebrush steppe, topographic heterogeneity creates heterogeneity in precipitation, with small mountain ranges east of the Cascades receiving more moisture than the surrounding basins. While the range of mean annual precipitation is similar in both regions, areas that receive less than 200 mm annually cover 36% of the Patagonian study area, but only 5% of the sagebrush steppe study area (excluding shrub-dominated areas)) (Fig. 2.2). This difference remains when all temperate areas of North and South America are included in the analysis, with 20% of temperate South America receiving less than 200 mm annual precipitation, compared to 7% of North America (Paruelo et al. 1995).

Comparing temperatures reveals stronger contrasts. Sites in the sagebrush steppe show greater thermal amplitude—hotter summers and cooler winters—than sites in Patagonia (Fig. 2.2). This potentially important difference is obscured by simple comparisons of mean annual temperature.

Focusing on long-term data from ALE and RM reinforces these trends: patterns in precipitation quantity and timing are quite similar, with the vast majority of moisture received during fall through spring in both regions, but the sagebrush site has greater thermal amplitude than the Patagonian site (Fig. 2.3A,B). The higher summer temperatures at ALE result in a higher annual mean, 11.9°C compared to 8.6°C at RM. The temperature difference is smaller during the spring growing season, which begins when temperatures increase enough to allow photosynthesis and ends when soil moisture from the winter rains is exhausted.

A second important difference is the higher wind speeds in Patagonia (Fig. 2.3C). Although both regions are dominated by westerlies that reach their greatest strength during spring, mean monthly velocities are often more than twice as high at RM than at ALE. This inter-site difference characterizes the broader regional comparison as well.

Geology and soils

The sagebrush and Patagonian steppes share strikingly similar geology. The Cascades and Andes were both created by the subduction of an oceanic plate under the leading edge of a continental plate (Engebretson et al. 1985, Ramos 1989). This process, which began in the late Miocene in Patagonia (Solbig 1973) and the Pliocene in the sagebrush steppe (Jensen et al. 1997), generated the cone shaped, still-active volcanoes characteristic of both ranges. Basalt flows, dating back to the Miocene in both regions, and granitic rocks scoured from the mountains by glaciers provided the parent material for soils, although in Patagonia older (Jurassic) volcanics are common on the Santa Cruz plateau and Tertiary marine sediments dominate some coastal areas (Mapa Geológico de la República Argentina 1997). Most contemporary surfaces originated during the Pleistocene. During this period, glaciers directly affected only the margins of the sagebrush steppe, but winds deposited deep layers of loess (Daubenmire 1970, Jensen et al. 1997). In Patagonia, rivers spread Pleistocene conglomerates over the steppes and left the rounded stones ("rodados patagónicos") that are a ubiquitous feature in much of western Patagonia. The late Pleistocene and Holocene brought little geomorphologic change to Patagonia, in contrast to the repeated damming and flooding of glacial Lake Missoula 12-15,000 years ago that created the channeled scablands in the Columbia Plateau of eastern Washington.

Comparing the distribution of soil types in each region reveals the influence of both geological history and climate. The most striking difference is the larger area of Aridisols in Patagonia compared to sagebrush steppe (38% vs. 21%) and the smaller area of Mollisols (21% vs. 36%) (Table 2.1). This difference reflects the greater area of extremely arid climate within Patagonia. A second difference is the greater abundance of older, more developed soils in Patagonia (Haplargids, Paleorthids), perhaps due to preservation of some pre-Quaternary surfaces and the relative lack of Holocene geologic activity. The abundance of sodium-affected soils in Patagonia (Natragids) is likely a result of a greater marine influence, while the large area of Cryoborolls in sagebrush steppe is concentrated entirely within Wyoming, the portion of the sagebrush steppe with the coldest, most continental climate.

Soil texture also differs to some degree between regions. The most common soils in the sagebrush steppe are silty loams, loams, and sandy loams, while Patagonian soils tend to be coarser, with sandy loams and loamy sands most abundant (Fig. 2.4). In Patagonia, 78% of soils are "sandy," compared to only 29% in the sagebrush steppe.

Evapotranspiration

The twelve weather years from ALE and RM selected as model input are well matched in terms of annual precipitation (Fig. 2.5), and are representative of long-term precipitation seasonality at each site (Fig. 2.6).

In simulations using either ALE or RM soils, the hotter ALE summer temperatures caused a small increase in bare soil evaporation, and decrease in transpiration, compared to runs using RM temperature and precipitation (Table 2.2). Substituting the strong RM winds for lighter ALE winds caused an increase in evaporation and decrease in transpiration of almost the same magnitude. The sandier soils at the RM site allowed consistently more efficient use of precipitation (higher percentage of AET is transpiration) no matter which weather inputs were used (Table 2.2).

The seasonality of water losses was insensitive to the small differences in climate, and also to differences in soil texture. Under all scenarios, evaporation peaked in early to mid spring, while transpiration peaked in late spring and early summer (Fig. 2.7). Using RM climate (temperature, precipitation, and wind), transpiration was marginally higher during late summer and fall, but marginally lower during early summer, than with ALE climate (Fig. 2.7). Transpiration peaked at higher values on RM soils than ALE soils, but evaporation peaked at a slightly higher value on ALE soils.

NDVI

Mean NDVI was 0.24 and 0.19 in sagebrush grass and grass-shrub areas, respectively, and 0.24 and 0.17 in Patagonian grass and grass-shrub areas. However, peak NDVI was higher in sagebrush than Patagonian steppe for both vegetation types and occurred during the month of the summer solstice for all areas except the Patagonian grass-shrub region, which peaked one month earlier (Fig. 2.8A). Because of the different data sources used for North and South America, these comparisons, based on absolute NDVI values, should be viewed with caution.

Comparisons of seasonality, in contrast, are not influenced by the difference in data sources. Seasonal NDVI dynamics in sagebrush steppe feature a steep climb to a well-defined peak, followed by a rapid decline. In Patagonia, the springtime increases in

NDVI are also steep, but the peak is followed by a more gradual decline (Fig. 2.8B,C), suggesting a longer growing season than in sagebrush steppe.

DISCUSSION

Summary of main similarities and differences

The comparison of climate, past and present, reveals very strong similarities in historical and contemporary precipitation regimes. The onset of the current arid and semiarid, winter precipitation climates began in the mid-Pliocene in both regions, and the current seasonal distributions of precipitation match well. Although the precipitation gradients in both regions span virtually the same range, areas receiving less than 200 mm annually are more extensive in Patagonian than sagebrush steppe. Additional climatic differences include greater thermal amplitude in sagebrush steppe and stronger winds in Patagonia.

The comparison of geology and soils also revealed important similarities. Because of similarity in the underlying geology of the Cascades and Andes, the parent material for soils in both regions is similar, and the timing of erosional deposition also matches well. However, the relative importance of aeolic processes in sagebrush steppe (West 1983) produced large areas of soils dominated by silts, while alluvial processes in Patagonia led to extensive areas of sand-dominated soils. A second, quite subtle difference is evidence of younger, less developed soils in sagebrush steppe, perhaps because of greater late Pleistocene geologic and geomorphologic activity relative to Patagonia.

Ecological importance

Because water is the most frequent limiting resource for ecological processes in grasslands and shrublands (Noy Meir 1973), similarities in precipitation are of overwhelming importance and produce strong convergence in the structure of plants and communities. By the same token, the differences in the spatial distribution of precipitation will be important as well, and could have implications for plant evolution. Isolation offered by the large and homogeneous arid zone in Patagonia might have promoted the evolution of plant traits that confer resistance to drought, such as short stature, basal meristems, and sclerophylly (Coughenour 1985). In the sagebrush steppe, in contrast, the small, scattered pockets of true aridity might have received too much gene flow from adjacent productive areas to permit evolution of extremely xerophytic varieties.

The ecological importance of differences in temperature, wind, and soils depend on their effects on water availability, which I used the soil water model to evaluate. This analysis, which held vegetation constant, showed that the climate differences were not as important as the soil differences. The drying effect of hot summers in sagebrush steppe was offset by the drying effect of high spring and summer winds in Patagonia, so that modeled evaporation and transpiration were similar given wind and weather typical of each region. The greater thermal amplitude in North America did have a small effect on the timing of evaporation and transpiration, which were higher in early spring and fall in Patagonia. These differences were subtle compared to the effect of soils. The sandy Patagonian soils allowed higher precipitation use efficiency, as measured by transpiration/evaporation, presumably because water reached deeper soil layers and was protected from evaporation.

The results of the model were consistent with previous simulations for Patagonia. Paruelo and Sala (1995), using a different model, found that transpiration averaged 34% of actual evapotranspiration (AET) at RM for 19 simulated years. My model runs using RM climate and soils also showed that transpiration averaged 34% of AET (Table 2.2).

Since the soil water model uses growing season length as an input variable, I turned to NDVI to look at how differences in temperature and soils might influence the seasonal dynamics of vegetation. Consistent with the results of the soil water model, the NDVI analysis suggested greater activity of vegetation in Patagonia during summer and fall. The longer growing seasons observed in Patagonian vegetation types are likely the result of lower summertime temperatures and coarser soils promoting deeper soil water, both factors that will reduce evaporative losses relative to sagebrush steppe. The NDVI results show that Patagonian plants take advantage of this extended period of water availability, and do not senesce as rapidly as plants in sagebrush steppe.

A second difference in NDVI was the higher values in sagebrush compared to Patagonian steppe. One explanation for the higher North American values may be above average precipitation during the period of the NDVI record. In some parts of the sagebrush steppe, 1995 and 1996 were the two wettest years on record (Hoitink et al. 1999). In these water limited systems, increased precipitation will result in increased leaf area and higher NDVI values. Such anomalous wet years did not occur during the period of observation in Patagonia. Furthermore, given its longer duration, the Patagonian record would be less sensitive to extreme events. Additionally, the very low NDVI values of the grass-shrub zone in Patagonia reflect the greater extent of this vegetation type receiving less than 200 mm mean annual rainfall.

Higher NDVI values in North America are not a result of using 1 km LAC data for sagebrush steppe and 8 km PAL data for Patagonian steppe. Comparisons of 1 km and 8 km values for regions of homogeneous native vegetation in North America, where both data sources are available, showed that the 8 km data values tended to be higher (unpublished data), a result of using maximum pixel values to aggregate the raw data up to the 8 km resolution (Agbu and James 1994). Therefore, the difference in data sources probably decreases rather than increases the difference between sagebrush and Patagonian steppe NDVI values.

In addition to their influence on seasonal vegetation dynamics, the soil differences I identified may have effects on nutrient availability. Although I found some evidence of better-developed soils in Patagonia, given the similarity in soil parent material and age it is unlikely that Patagonian soils have suffered greater nutrient losses to weathering. The coarser soils of Patagonia, however, could create nitrogen limitation. Sandy soils have higher nitrogen mineralization rates and accumulate less total nitrogen than finer textured soils (Schimel et al. 1985a,b, Aguilar and Heil 1988, Aguilar et al. 1988) that may stabilize more N through adsorption and aggregation onto clays (Schimel et al. 1985a). Lower total N and higher N losses on sandy soils could lead to nitrogen limitation.

Differences in growing season length and N supply would have implications for two important ecological issues in both regions, the effect of domestic livestock grazing on vegetation, and vulnerability to exotic plant invasions. Plant defenses against grazing, whether chemical or morphological, often involve a trade-off with growth (van der

Meijden et al. 1988, Herms and Mattson 1992, Grime et al. 1997). A system with a short growing season such as the sagebrush steppe might require fast growth, and thus make defense strategies costly. A longer growing season, as in Patagonia, might remove constraints on defensive strategies and permit the evolution of plants better adapted to avoid herbivory, resulting in a more grazing resistant plant community. The potential for N limitation in coarse soils might further increase the likelihood of finding effective plant defenses in Patagonia, since losses of leaf-tissue to herbivores could be more difficult to replace (Coley et al. 1985). Potential N limitation would also have important consequences for the success of exotic plant invaders, which typically perform best on high nutrient sites (Lauenroth et al. 1978, Harrison 1999, Stohlgren et al. 1999). If the coarser soils of Patagonia lead to N limitation, we should predict that Patagonian steppe, or at least areas of Patagonia with extremely sandy soils, should be more resistant to invasion than sagebrush steppe. N limitation might play a role in the failure of the invasive annual grass *Bromus tectorum* to expand its range as dramatically in Patagonia as it has in sagebrush steppe (Mack 1981, Novak and Mack 2001).

My results demonstrate that even when overall climatic and physical similarity between ecosystems is strong, as in the case of the sagebrush and Patagonian steppe, small abiotic differences will inevitably exist. These subtle contrasts have the potential to exert strong influences on particular ecological processes, such as plant invasions. The presence of such differences will complicate continental comparisons, but should not preclude this powerful approach for testing theory. After all, the abiotic environments of the sagebrush and Patagonian steppe impose essentially the same ecological challenges on the organisms living in these regions. But before ascribing differences in ecological structure and function to differences in the evolutionary history of these ecosystems, we should consider alternative explanations based on the unavoidable environmental differences. This may require a series of manipulative experiments designed to reject the causal roles of particular abiotic mechanisms.

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Table 2.1. Common soils of the sagebrush steppe, North America, and Patagonian steppe, South America. Shown are Great Groups covering at least 2% of the total area of each region.

Sagebrush steppe		Patagonian steppe	
Great Group	Area (%)	Great Group	Area (%)
Cryoborolls	11.2	Torriorthents	17.0
Torriorthents	10.8	Paleorthids	10.7
Argixerolls	8.9	Haplargids	10.3
Haplargids	8.8	Rock	10.1
Haploxerolls	5.5	Haploborols	7.9
Argiborolls	3.9	Natrargids	7.5
Cryochrepts	3.8	Vitrandepts	5.7
Camborthids	3.5	Xerorthents	5.0
Calciorthids	3.0	Argixerols	4.0
Torripsamments	2.9	Haploxerols	3.9
rock	2.9	Paleoargids	3.7
Cryoboralfs	2.8	Calciorthids	2.4
Xerochrepts	2.3	Camborthids	2.1
Ustorthents	2.3		
Durargids	2.1		
Total shown	74.8	Total shown	90.2

Table 2.2. Results from the soil water model simulations. Shown are means (mm) from 12 independent one-year runs. "Weather" refers to daily temperature and precipitation. ALE soil initiated at 80% of wilting point each year, RM at 75%.

weather	wind	Evap.	Transp.	AET	Soil water	T/AET
Using ALE soils						
ALE	ALE	107.9	49.8	157.8	-0.3	0.32
ALE	RM	113.3	45.4	158.7	-1.3	0.29
RM	ALE	102.6	52.6	155.2	3.9	0.34
RM	RM	108.4	48.8	157.2	2.0	0.31
Using RM soils						
ALE	ALE	104.7	57.8	162.5	-5.1	0.36
ALE	RM	110.6	55.0	165.6	-8.2	0.33
RM	ALE	99.4	55.5	154.9	4.2	0.36
RM	RM	104.8	54.8	159.6	-0.5	0.34

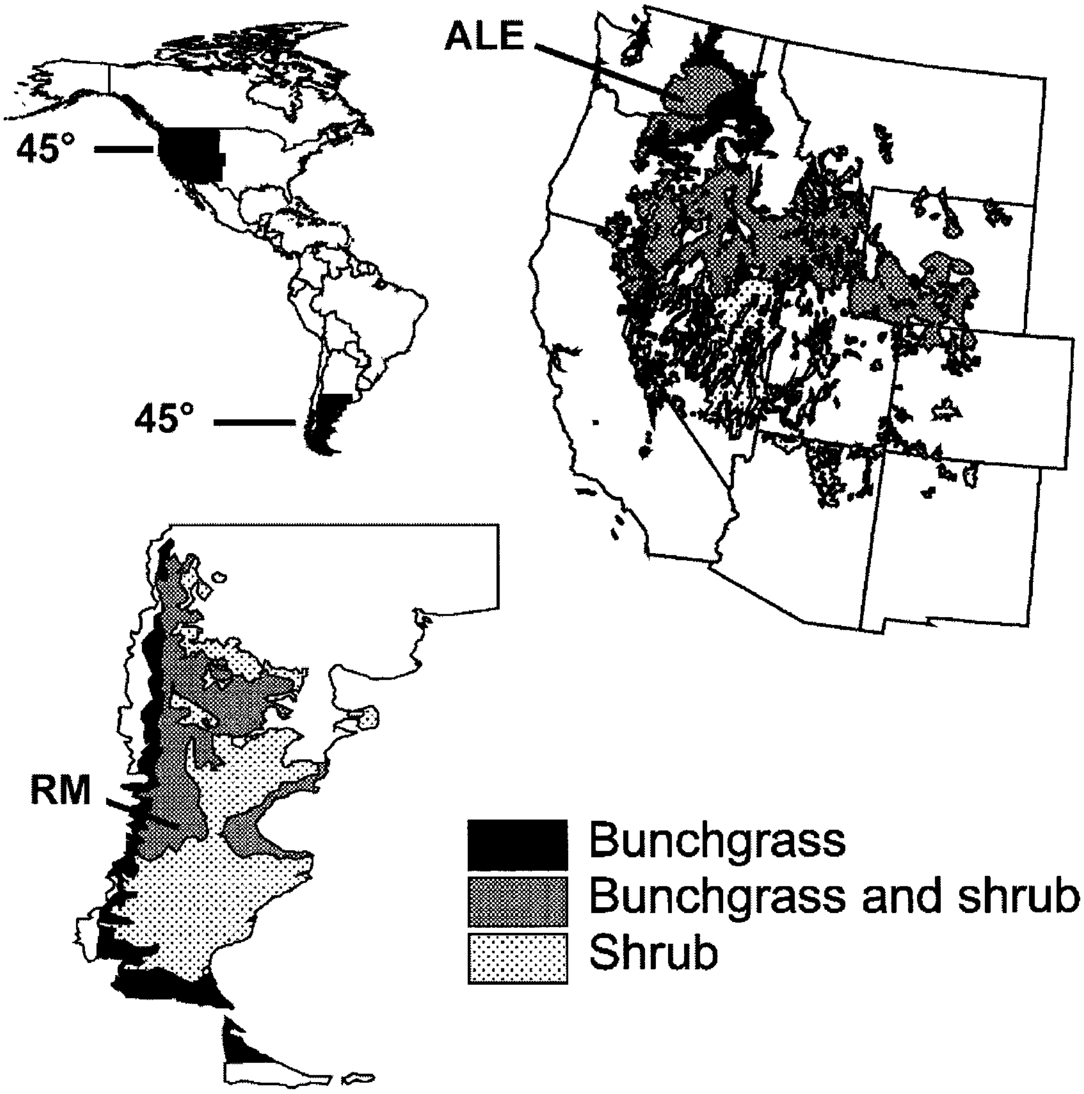

Fig. 2.1. Arid and semiarid vegetation types of the Intermountain west of North American and the Patagonian region of South America (based on Küchler 1964 and León et al. 1998). Also shown are the locations of the Arid Lands Ecology reserve (ALE) in North America, and the Río Mayo Experimental Station (RM) in South America. Analyses were based on the bunchgrass and bunchgrass and shrub vegetation types and excluded the shrub-dominated zones.

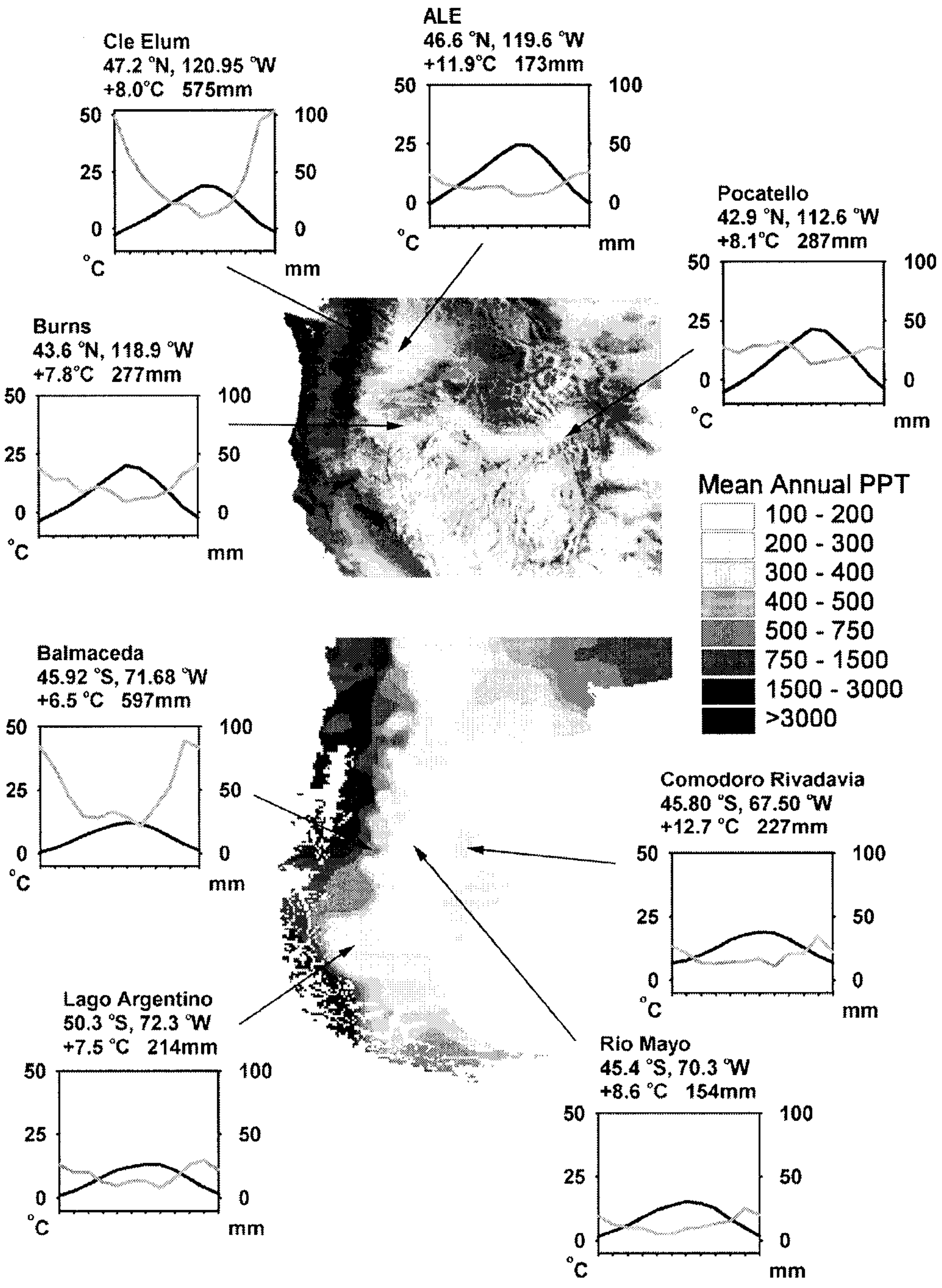

Fig. 2.2. Mean annual precipitation maps for the sagebrush and Patagonian steppes, and detailed climate diagrams for selected locations (the horizontal axes show months January-December for sagebrush steppe and July-June for Patagonia). The sagebrush steppe precipitation map is based on Daly et al. (1994), and the Patagonia map is an interpolation based on over 60 weather stations.

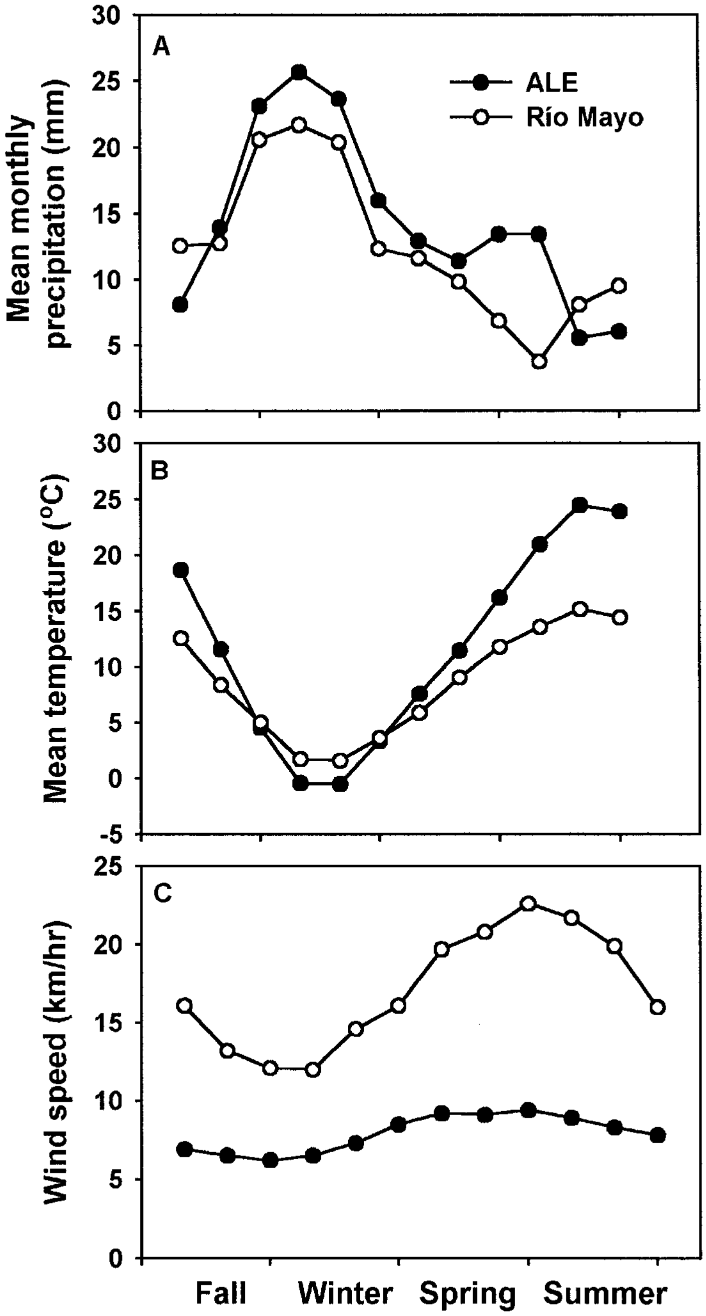

Fig. 2.3. Mean monthly precipitation (A), temperature (B), and wind speed (C) at the Arid Lands Ecology reserve (ALE) in the sagebrush steppe, and the Río Mayo Experimental Station (RM) in Patagonian steppe. Data are from Hoitink et al. (1999) for ALE and Beltrán (1997) for RM.

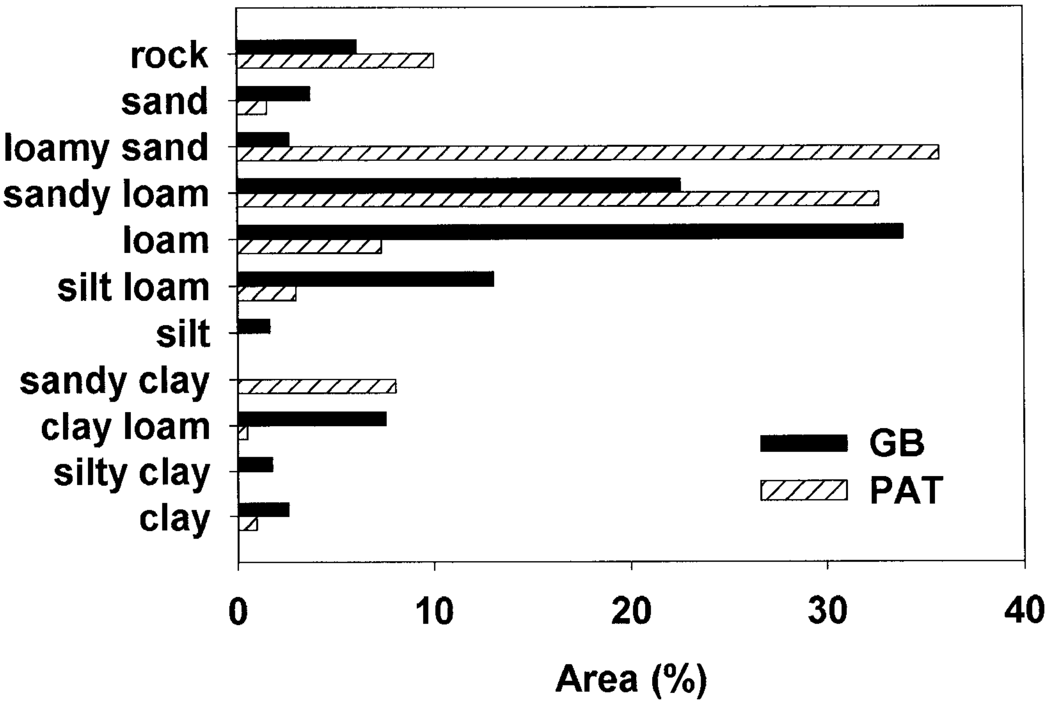

Fig. 2.4. Soil texture by area in sagebrush (SGBR) and Patagonian (PAT) steppe. Analysis is based only on areas of dominated by grasses or grasses and shrubs (see Fig. 2.2.1).

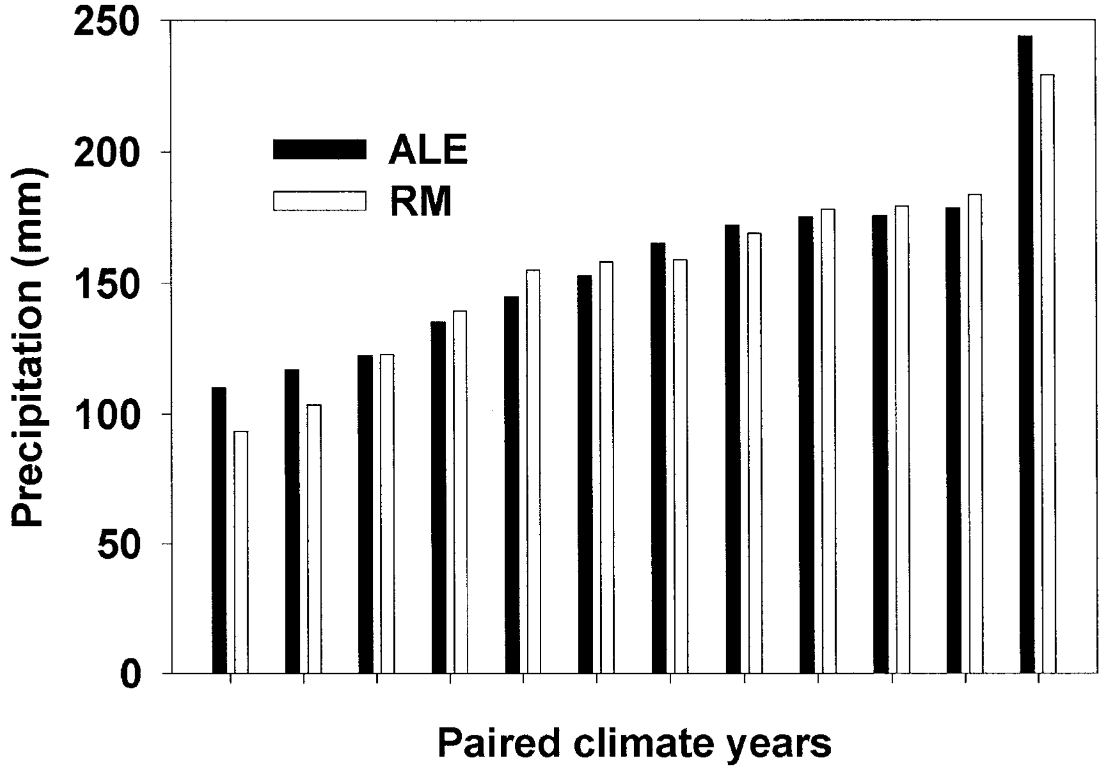

Fig. 2.5. Annual precipitation in a sagebrush (ALE) and Patagonian (RM) site for the twelve pairs of climate years used as input for the soil water model, arranged in order of increasing precipitation.

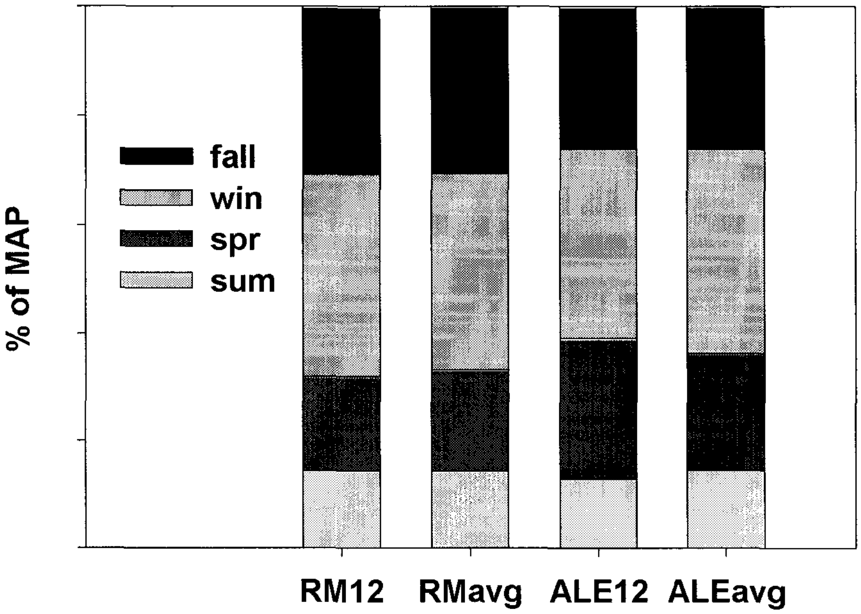

Fig. 2.6. Mean precipitation seasonality in the twelve years used in the soil water analysis and the long-term average for a Patagonian (RM12 and RMavg) and sagebrush steppe site (ALE12 and ALEavg).

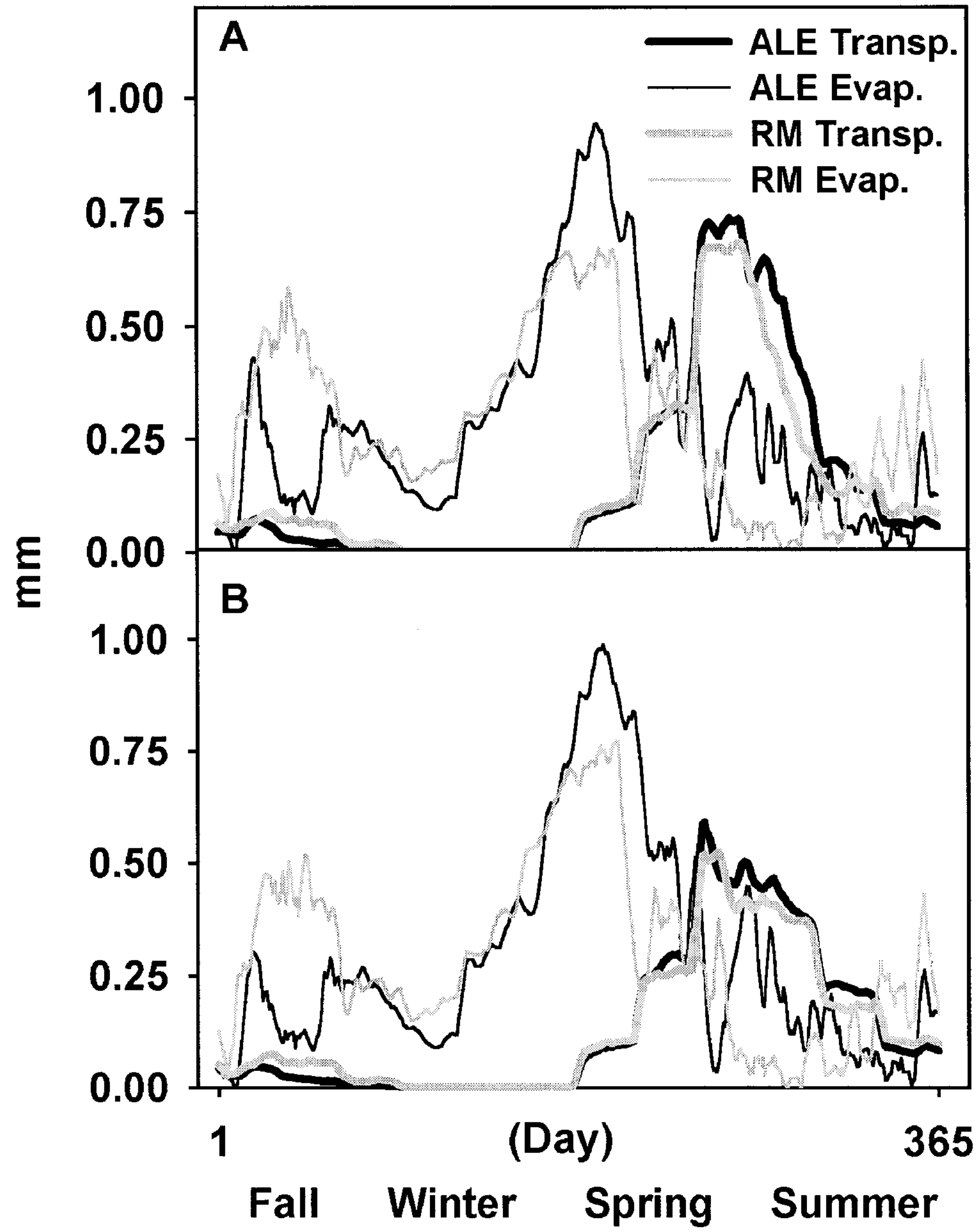

Fig. 2.7. Results from the soil water model analysis. Panel A) shows runs using RM (Patagonian site) soil parameters, and B) shows runs using ALE (sagebrush site) soil parameters. The lines are 5-day running averages of modeled mean (*n* = 12) daily transpiration and evaporation using ALE weather and wind or RM weather and wind. Day 1 corresponds to September 1 in ALE and March 1 in RM.

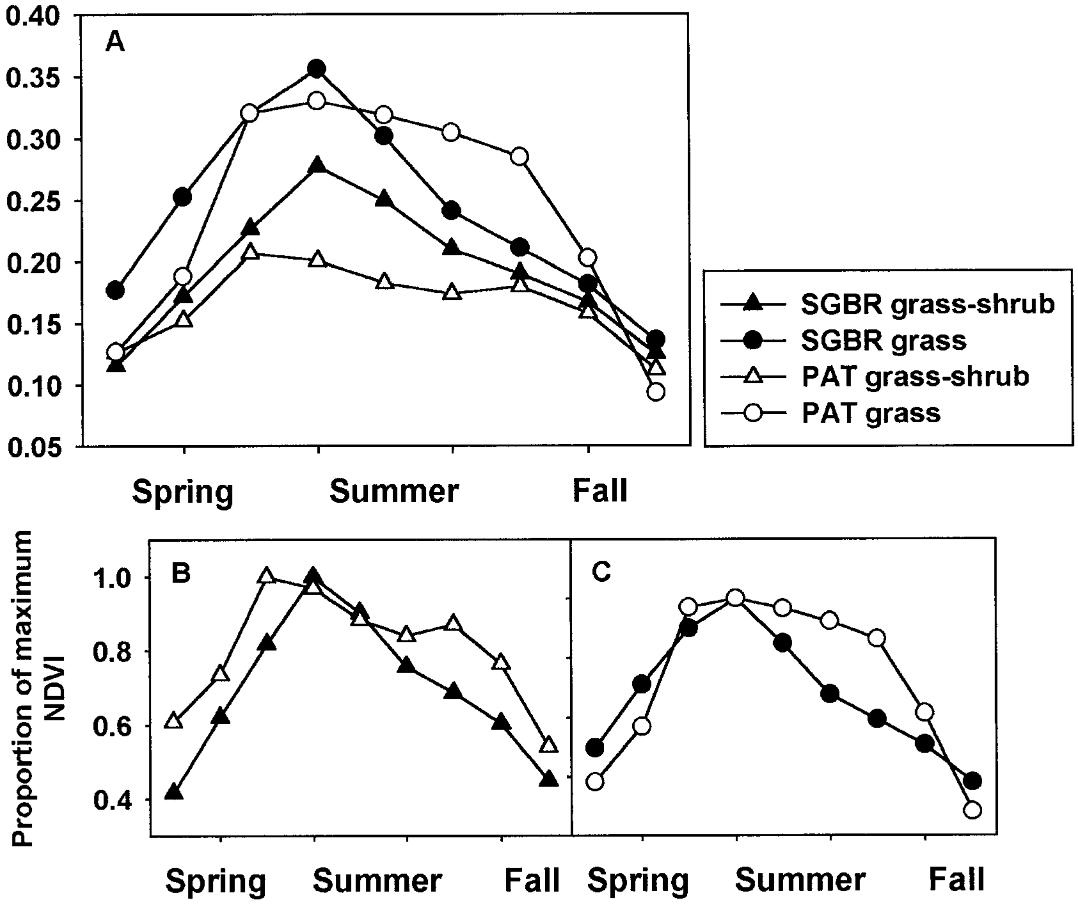

Fig. 2.8. Satellite-derived mean monthly NDVI for grass and grass-shrub vegetation types in sagebrush and Patagonian steppe (shown in Fig. 2.1). A) Mean NDVI values, based on 1x1 km data for sagebrush steppe, and 8x8 km data for Patagonia. B) NDVI for grass-shrub dominated areas in each region standardized by dividing each curve by its maximum value. C) NDVI for grass-dominated areas, standardized as in B.

CHAPTER 3: FUNCTIONAL TRAITS AND GRAZING RESISTANCE IN GRAMINOIDS OF SAGEBRUSH STEPPE, USA AND PATAGONIAN STEPPE, ARGENTINA

ABSTRACT

Analyses of plant functional traits can provide predictions about ecosystem response to grazing and, since traits are legacies of historical selection pressures, may demonstrate the importance of a plant community's evolutionary history of grazing. I measured grazing tolerance and avoidance traits of graminoids collected in the Patagonian steppe of Argentina, the sagebrush steppe of the northwestern U.S., and the shortgrass steppe of the central U.S. to, first, make inferences about the role of evolutionary history of grazing in determining functional traits and, second, generate predictions about the vulnerability of these ecosystems to grazing impacts. To measure grazing tolerance, I conducted a greenhouse defoliation experiment on dominant grasses from each region. The poor performance of *B. gracilis*, a species extremely well adapted to grazing under field conditions, suggests that either tolerance is less important than avoidance in determining plant population responses to grazing, or greenhouse conditions fail to reproduce field responses. To compare avoidance-related traits, I measured both morphological traits and leaf chemical composition on common species from each region, then performed a Principal Components Analysis on the species by traits matrix.

The first axis of the ordination was correlated with measures of forage quality such as leaf tensile strength, fiber, and N content, while the second axis was correlated with plant stature. The dominant species from the most arid Patagonia site scored significantly lower on the first axis (low forage quality) than dominants from the sagebrush steppe. Plants from the wetter Patagonia site and the shortgrass steppe species were intermediate in forage quality. Sagebrush steppe species scored significantly lower on the second axis (taller), though this difference was not significant when I considered only dominant species. These differences are consistent with evidence indicating that large ungulates were rare in eastern Washington during the late Holocene, but guanaco were ubiquitous in Patagonia. However, subtle differences in environmental factors offer alternative explanations for the evolution of apparent grazing defenses in Patagonia. Regardless of their origin, these differences in traits can explain why the introduction of domestic livestock has had different effects on vegetation in these ecosystems.

INTRODUCTION

Recent research attempting to explain the great variability in ecosystem response to grazing (Milchunas and Lauenroth 1993) has focused on the role of plant functional traits. The general hypothesis states that grazing resistance depends on the frequency and strength of adaptations that allow plants to avoid or tolerate herbivory (van der Meijden et al. 1988, Díaz et al. 1992, Lavorel et al. 1999, McIntyre et al. 1999, Díaz et al. 2001, McIntyre and Lavorel 2001, Vesk and Westoby 2001). This hypothesis predicts that grazing impacts will be smaller in systems where traits conferring resistance to grazing are well developed and common among plant species than in systems where such traits are poorly developed or rare. Although previous work has identified certain key traits such as life form, plant stature, seed size, and leaf toughness (Milchunas and Lauenroth 1993, Díaz et al. 2001, McIntyre and Lavorel 2001), cross-system generalizations appear elusive (Vesk and Westoby 2001). Questions still remain about the relative importance of various traits, such as those related to grazing avoidance versus tolerance (McIntyre et al. 1999), and how their importance may change in different ecological contexts.

Even if research on plant traits advances to allow quantitative predictions of grazing response, understanding differences among ecosystems requires identifying the origins of differences in plant traits. Two factors are particularly important in creating grazing-resistant traits: aridity and the evolutionary history of grazing. Adaptations to aridity such as small stature, basal meristems, and drought-deciduous leaves also prove advantageous in preventing or recovering from herbivory (Coughenour 1985). In the context of grazing defense, these traits can be viewed as "exaptations" rather than adaptations (Gould and Lewontin 1979). The evolutionary history of grazing (Larson 1940, Stebbins 1981, Mack and Thompson 1982, Milchunas et al. 1988) refers to the history of selection pressures on plants exerted by populations of generalist herbivores. Grazing-resistant traits that evolve in response to these selection pressures are true adaptations to grazing.

The evolutionary history of grazing concept has influenced grazing research for more than two decades (Mack and Thompson 1982, Milchunas et al. 1988), yet it remains more of a thinking tool than a quantitative predictor. Testing predictions based on a system's evolutionary history is problematic because quantifying it is so difficult. Milchunas and Lauenroth (1993) relied on subjective estimates of the length of the evolutionary history of grazing to generate predictions about ecosystem response. Such estimates require information on historical populations of native herbivores over some relevant time period, typically assumed to be on the order of millenia (but see Burkhardt 1996). Even when this information is available, predictions about present day plant community responses depend on the untested assumption that native herbivore populations had strong effects on the development of plant traits in the contemporary flora.

We can circumvent these problems by restating the Milchunas et al. model to make explicit the role of plant functional traits. Instead of predicting the plant community response to grazing based on aridity and evolutionary history, we should specify two separate hypotheses. First, both the evolutionary history of grazing and environmental factors determine plant traits, and second, plant traits determine the response to grazing (Fig. 3.1). More elaborate versions of this conceptual model might recognize the feedbacks of plant traits on evolutionary history and of contemporary grazing response on plant traits.

Compared to evolutionary history of grazing, plant traits are easily measured, making possible rigorous tests of predictions generated by the second hypothesis. However, evaluating the first hypothesis will remain a challenge because of difficulties in quantifying evolutionary history and unraveling its interactions with environmental factors. In some cases, especially when information on historic herbivore populations is limited, we may choose to use plant traits to make inferences about the intensity of the evolutionary history of grazing. This approach assumes that since plant traits are the legacy of historical selective pressures, the frequency and degree of development of grazing-resistant traits will provide evidence for the length and intensity of evolutionary history of grazing. The disadvantage of this approach is that we can never be sure that grazing, and not other selective pressures, led to the observed adaptations, nor can we be sure that we have measured the most important functional traits. Inferences about evolutionary history based on plant traits can complement research that tests predictions about plant traits based on historical herbivore populations. Moving in both directions along this causal pathway will increase our understanding of the role of evolutionary history of grazing in driving plant evolution.

To demonstrate how plant traits relate to both hypotheses, I compared traits of common graminoid species from the Patagonian steppe of South America and the sagebrush steppe of North America. These two ecosystems are particularly appropriate for such a comparison. First, because of the strong influence of aridity on traits relevant to grazing resistance, climate will confound any trait comparisons. The temperate, semi-arid sagebrush and Patagonian steppes have very similar climates (Paruelo et al. 1995) and, as a result, show convergence of dominant plant growth forms (caespitose perennial grasses and shrubs) and ecosystem function (Paruelo et al. 1998). Large contrasts in plant traits, therefore, are likely to be the result of other selection pressures such as grazing. Second, domestic livestock grazing is an important land-use and evolutionary grazing history a debated topic in these regions. While Milchunas et al. (1988) used both of these ecosystems as examples of semi-arid systems with short evolutionary grazing histories, subsequent papers from Patagonia (Lauenroth 1998) and central Argentina (Pucheta et al. 1998, Díaz et al. 2001) noted apparent adaptations to grazing in the vegetation, suggesting a more intense history of grazing. The importance of guanaco

(*Lama guanicöe*), a native camelid, to the indigenous peoples of Patagonia, and the number of guanaco hides harvested by modern hunters, support this hypothesis (Franklin 1981). In contrast, there is strong consensus that ungulate numbers on the sagebrush steppe were very low during the last 2,000 years preceding European settlement, probably due to a combination of low productivity, dispersal barriers, and human hunting (van Vuren 1987, Lyman and Wolverton 2002). If, in fact, grazing has been a more important selection pressure in the Patagonian steppe than in the sagebrush steppe, graminoids from Patagonia should better tolerate and/or avoid herbivory.

Along with the Patagonian and sagebrush steppe species, I used graminoids from the shortgrass steppe of eastern Colorado, a system with a presumed intense evolutionary history of grazing (but distinct climate) to provide a known reference point for comparison. Because of the difficulty of screening many species for unknown secondary compounds, I limited the comparison to grasses, which are less likely to depend on this type of defense (Coughenour 1985, Vicari and Bazely 1993, but see Redak 1987). The comparison included a greenhouse defoliation experiment to assess grazing tolerance, and a multivariate analysis of physical and chemical traits to evaluate avoidance. I used the observed trait differences to, first, make inferences about the relative intensity of evolutionary history of grazing in sagebrush and Patagonian steppe and, second, to generate predictions about the relative impact of domestic livestock grazing in these ecosystems.

METHODS

Climate comparison and site descriptions

The Patagonian steppe of southern Argentina and the sagebrush steppe of North America occupy rain-shadow deserts created by the Andes and Cascade mountain ranges, respectively. Both ranges, located on the western edge of their continents, are the result of an oceanic plate being subducted beneath a continental plate (Engebretson et al. 1985, Ramos 1989). Similar parent material, derived from basalt lava flows and granitic intrusions, and patterns of volcanism occur in the southern Andes and the Cacades. Climate in both regions is characterized by warm, dry summers and cool wet winters, though moisture is concentrated on the west side of the mountains and decreases dramatically along a gradient extending east into the lower elevation steppes. Vegetation changes rapidly along the gradient of decreasing precipitation, with forests giving way to grasslands, and then grass-shrub steppes.

Despite the similarity in climate at the macro-climatic scale (Paruelo et al. 1995), detailed comparison reveals subtle but potentially important differences (Chapter 2). First, while the seasonal distribution of rainfall is quite similar, the limited landmass of temperate South America means that the maritime influence is stronger; Patagonian sites typically have weaker thermal amplitude, with milder winters and much cooler summers than sagebrush steppe sites (Fig. 3.2). Second, while some areas of central Washington state receive as little as 150 mm of precipitation annually, the extent of lands receiving less than 200 mm is much larger in Patagonia than in the sagebrush steppe. Finally, winds are much stronger in Patagonia (Fig. 3.3), especially during the spring growing season, and contribute to the region's aridity (Soriano 1983). Simulations with a soil water model indicated that these strong winds have a drying effect equivalent to the hotter summer temperatures of sagebrush steppe sites (Chapter 2).

I selected two study sites in Patagonia and two in sagebrush steppe, one at the grass-dominated, subhumid end of the precipitation gradient, the other in more arid zones dominated by both shrubs and grasses. The "wet" sagebrush steppe site is located west of the town of Grand Coulee, WA, at approximately 48°N and 119.3°W and 800 m elevation, on glaciated silty loam soils. Mean annual precipitation is at least 300 mm (Daly et al. 1994, data from local ranchers) and mean annual temperature 7.5°C (based on nearby Waterville, WA weather station). Vegetation in this Idaho fescue-three tipped sagebrush community (Daubenmire 1970) is dominated by the perennial bunchgrasses *Agropyron spicatum* and *Festuca idahoensis*, and *Artemisia tripartita* is the most common shrub (botanical nomenclature follows Hitchcock and Cronquist 1973). The "dry" sagebrush steppe site is Wanapum State Park, near the town of Vantage, WA (47°N, 120°W, 300 m elevation). Soils are unglaciated silty loams. Mean annual precipitation is approximately 175 mm and mean annual temperature 12° C (based on nearby Arid Lands Ecology Reserve weather station shown in Fig. 3.2). The dominant species are *Agropyron spicatum* and the shrub *Artemisia tridentata* var. *tridentata*, representative of the most widespread sagebrush steppe community type (Küchler 1964, Daubenmire 1970). I refer to these two vegetation types collectively as sagebrush steppe.

The "wet" Patagonia site is located in southwest Chubut province, Argentina, at 46°S, 71.5°W, 650 m elevation, on glaciated silty loam soils. Mean annual precipitation is 400 mm (data from local rancher) and mean annual temperature is 6.5°C (from Balmaceda, Chile, weather station). Vegetation, corresponding to the sub-Andean grass steppe community (León et al. 1998), is dominated by the perennial bunchgrass *Festuca pallescens* and the most common shrub is *Mulinum spinossum* (botanical nomenclature follows Correa 1969-1999-). The "dry" Patagonia site is in central Chubut province at the Río Mayo Experiment Station of Argentina's Instituto Nacional de Tecnología Agropecuaria (INTA) (45.4°S, 70.3°W, 500 m elevation). Soils are alluvial derived sandy loams. Mean annual precipitation is 154 mm and mean annual temperature 8.6°C (Beltrán 1997). Vegetation is representative of the Occidental District (León et al. 1998). The dominant perennial grasses are *Stipa speciosa*, *Stipa humilis* and *Poa ligularis*, and the dominant shrubs are *Mulinum spinossum*, *Adesmia campestris*, and *Senecio filaginoides*. The shortgrass steppe site is at the Central Plains Experimental Range (40.8°N, 107.8°W) in northeastern Colorado. Mean annual precipitation is 324 mm, of which 85% falls in May, June, and July, in contrast to the winter precipitation of the Patagonia and sagebrush steppe sites. Mean annual temperature is 8.6°C and soils are generally coarse in texture. The vegetation is dominated by the short, C_4 perennial grasses *Bouteloua gracilis* and *Buchlöe dactyloides* (no C_4 grasses are important in Patagonian or the sagebrush steppe) while *Agropyron smithii* is the most common C_3 grass.

Defoliation experiment

I collected dominant plant species from each study site to propagate in the greenhouse. I used *S. speciosa*, *S. humilis* and *P. ligularis* from the dry Patagonia site, and *F. pallescens* from the wet Patagonia site. Sagebrush steppe plants included *A. spicatum*, *Poa sandbergii*, and *Stipa thurberiana* from the dry site, and *F. idahoensis* from the wet site. In addition, I collected *B. gracilis* and *A. smithii* from the shortgrass steppe site. Four individual plants of each species were randomly selected from ungrazed exclosures or areas of pastures seldom visited by livestock (only *F. pallescens* and *F. idahoensis*). After washing the roots and separating the plants into smaller groups of tillers, I transplanted them into pots at the Colorado State University greenhouse.

In early March of 2002, I transplanted 30 individual tillers, each with 3 to 4 leaves, drawn from 2-3 clones of each species. I used plastic pots 10 cm in diameter and 35 cm tall. The growing medium was 50% sand and 50% vermiculite by volume. Pilot studies showed that the warm-season *B. gracilis* would grow and flower during the spring in the greenhouse, the optimum growth period for the C_3 grasses. From the initial planting until the end of the experiment, I watered plants twice a week to field capacity and once each week with 100 ml of 50% Hoagland's solution. Daytime temperatures throughout the experiment were maintained near 21.1°C, and nighttime temperatures kept above 15.6°C, with ambient light. I gave the transplants one month to acclimate. During this time, I removed all plants that died of transplant shock. For most species, less than 5 individuals died, but mortality was high among all *Stipa* species from both regions and I removed them from the experiment.

In early April, after the one-month acclimation period, I harvested six to ten randomly selected individuals of each species, depending on the number of surviving replicates, to determine initial above and belowground biomass. I randomly assigned 9 of the remaining 18 individuals of each species to a clipping treatment, and the remaining 9 to an unclipped control treatment, further stratifying by genotype within each species. Plants assigned to the defoliation treatment were clipped at 4 cm above the soil surface (following Polley and Detling 1990). Clipping at a constant height, rather than removing a constant proportion of biomass, retains an advantage for short stature species. I arranged the individual plants in a randomized complete block design, with one control and one defoliated plant of each species in each block (9 blocks total).

Three weeks after the initial clipping, I again clipped the defoliated plants to 4 cm (2 defoliations total). After another 3 weeks, I harvested all surviving replicates. Plants that died during the experiment (on average one per treatment per species) were not included in the analysis. I determined dry weight of all aboveground material, both clippings and final harvest, after it was dried for 48 hr in a 55°C oven. To determine belowground biomass, I first dried roots and surrounding soil from each replicate for 48 hr in a 55°C oven, then ashed the material for 5 hours at 525°C. I took the difference in pre- and post-ashing mass as belowground biomass.

The response variables I analyzed were total aboveground production (final biomass plus all clippings) and total belowground biomass (final biomass). I used a linear mixed model, with genotype nested within species as the random factor, and species and clipping treatment as the fixed factors (Proc Mixed, SAS 8.2, SAS Institute, 1999). Production data were log transformed; reported values were back-transformed. I did not have a sufficient number of species per region to include region as a fixed factor in the model.

Multivariate analysis of avoidance traits

While the defoliation experiment included only dominant species, I included all common graminoids at each site in the analysis of avoidance traits. In order to minimize the confounding effects of variation in grazing intensity, I used plants from long-term exclosures at the dry Patagonia, dry sagebrush steppe, and shortgrass steppe sites, and within recent (1 year old) exclosures located in lightly grazed areas in the wet Patagonia and sagebrush steppe sites. Thus, the comparison focuses on ungrazed plants only, and not on differences between grazed and ungrazed plants of each species.

I measured physical traits and collected biomass during 2001 near the end of each species' growing season as seeds began to harden but before plant senescence (January in Patagonia, May and June in sagebrush steppe, and July and August in the shortgrass steppe). This meant that some early phenology species, such as *P. secunda* in the sagebrush steppe, were harvested well before later-maturing species. To measure leaf tensile strength, a key trait that is negatively correlated to palatability and digestibility (Cornelissen et al. 1999), I built a spring-tensioned device modeled on Hendry and Grime's (1993). Immediately after collecting biomass, I placed mature green leaves in water indoors to prevent dessication. I measured the force required to tear a single leaf, recording leaf width and thickness at the location of the tear, with ten replicates for each species. I measured all remaining physical traits (Table 3.1) on the individual plant of each species growing nearest 10 pre-determined points on a line transect. The trait values for each species are the means of these ten measurements. After measuring physical traits, I harvested all ten plants of each species, and additional biomass if necessary, for subsequent laboratory analysis of chemical traits (Table 3.1).

To prepare plant tissue samples for chemical analysis, I separated 5 g of mature green leaves, blades and sheaths, of each species from each site and dried the sample for 48 hr at 55°C. Each sample was ground in a Wiley mill with a 1 mm screen. I used the van Soest (1982) method for fiber analysis, and sent the samples to the CSU Soil and Plant Testing Laboratory for analysis of C, N, P, and Si. C and N were determined by combustion using a LECO CHN-1000 (St. Joseph, MI), and P and Si by the nitric/perchloric acid digest method (Miller and Kotuby-Amacher 1996).

I performed a Principal Components Analysis (Canoco 4.0, 1998) on the sample by traits matrix. The PCA was based on between trait correlations, rather than covariances, since units of measurement varied among traits. The first version of the ordination excluded shortgrass steppe plants. To test for differences between Patagonian (PAT) and sagebrush steppe (SGBR) plants, I performed a two-way analysis of variance, with region (PAT or SGBR) and precipitation (wet or dry) as the factors, on scores from PCA axis 1, and a second ANOVA on scores from PCA axis 2. To test for between sites differences, I used post-hoc least squares differences (LSD), setting $\alpha = 0.05$. I repeated these tests considering only the scores of the 3 most abundant species at each site. The second version of the ordination included shortgrass steppe (SGS) species. To test for differences among species scores in this ordination, I used a one-way ANOVA on site (PAT wet, PAT dry, SGBR wet, SGBR dry, SGS) rather than the two-way test used on the first ordination. Again, I tested for differences among scores on both PCA axes 1 and 2, for all species and then just dominants, using the post-hoc LSD test. Results from both ordinations and subsequent ANOVAs were qualitatively similar, so although I describe results from the first ordination in the text, I only show figures from the second.

RESULTS

Defoliation experiment

Clipping had a negative effect on both above and belowground production of all species, but the significant species by treatment interaction for aboveground (F = 2.22, *p*

= 0.048) and belowground production (F = 5.9, $p < 0.0001$) indicates that clipping damaged some species more than others (Fig. 3.4). *B. gracilis*, a strong grazing increaser from the grazing resistant shortgrass steppe (Michunas et al. 1989), was less tolerant of grazing than all Patagonian and sagebrush species, with tolerance measured as defoliated/control aboveground production (Table 3.2). The least tolerant species overall, *A. smithii*, also came from the shortgrass steppe, where it generally decreases with grazing (Milchunas et al. 1989). There were no clear differences in tolerance between Patagonian and sagebrush steppe grasses.

Multivariate analysis of avoidance traits

The biggest differences among sites in terms of individual traits were in leaf and flower height, with Patagonian species tending to be shorter, and in leaf tensile strength and N concentration, with Patagonian plants tending to be tougher and lower in N (Table 3.3). The ordinations reflect these differences. In the ordination that excluded shortgrass steppe species, the first axis (PCA 1) was strongly correlated with traits related to palatability or digestibility such as C, lignin, and leaf tensile strength, which increased along the axis, and cell solubles and P, which decreased on the axis. The second axis (PCA 2) was positively correlated with measures of plant stature such as leaf and flower height. The first three ordination axes explained 28.7%, 23.6%, and 13.1% of total variance, respectively. In the ANOVA of PCA 1 scores, no differences among sites were detected when all species were included, but the model was significant (F = 13.9, p = 0.002, Table 3.4) when only the dominant 3 species from each site were considered. Region and the region by precipitation interaction were both significant. LSD comparisons showed that species from the Patagonian dry site had significantly higher scores on PCA 1 than species from any other site, indicating lower quality leaf tissue, and species from the Patagonia wet site had higher scores than species from the sagebrush steppe (Table 3.4). The ANOVA on PCA 2 scores was significant when all species were included ($F = 5.02$, $p = 0.006$), due to a strong difference between regions (Patagonian species tended to be shorter than sagebrush steppe species). Including only the dominants, the ANOVA was not significant (Table 3.4).

The ordination including shortgrass steppe species was qualitatively similar: the first axis was correlated with measures of leaf tissue quality such as N and tensile strength, while leaf length and plant height were associated with the second axis (Fig. 3.5). In this ordination, PCA axes 1 through 3 explained 24.5%, 23.0%, and 15.7% of variance, respectively. The ANOVA of PCA 1 scores for all species was not significant, but became significant when only the dominant species were included (Table 3.5). LSD comparisons showed that dominant species from the Patagonia dry site scored significantly lower, indicating lower quality tissue, than species from the sagebrush sites, but not lower than species from the Patagonia wet or shortgrass steppe sites (Fig. 3.6). The ANOVA on the PCA 2 scores of all species was significant (Table 3.5), with Patagonian species scoring higher, indicating shorter stature, than species from the three North American sites (Fig. 3.6). Using PCA 2 scores only for the dominant species, the model was not significant (Table 3.5).

Since leaf tensile strength integrates so many important structural and chemical traits, and since it varied so much between the Patagonian and North American sites, I thought it important to understand what creates tough grass leaves. Clearly, the thickness, or cross sectional area of the leaf should be important. A regression of leaf tensile strength on cross section did in fact show a significant, positive relationship, though the variance explained was low (Fig. 3.7). The trait that best accounted for the remaining variation was cellulose, explaining 52% of the variance in the residuals from the regression on cross section (Fig. 3.7). Tensile strength was not related to either silica or lignin content, which were low in all species.

DISCUSSION

Tolerance

Defoliation decreased above and belowground production for all species, regardless of their origin. More surprising is that species from the shortgrass steppe, the ecosystem known to have an intense evolutionary history of grazing, were the worst performers. That *A. smithii* tolerated clipping poorly might be expected, since it is a strong decreaser under grazing (Milchunas et al. 1989). *B. gracilis*, in contrast, increases in cover with heavy grazing, yet was less tolerant of clipping under greenhouse conditions than even *A. spicatum*, a sagebrush steppe species extremely sensitive to grazing (Daubenmire 1940, Rickard et al. 1975). Nor was *B. gracilis's* poor performance in this trial a fluke; its response during a warm season pilot study I conducted was similar. *B. dactyloides*, another shortgrass steppe grazing increaser, was included in this pilot study, and was only marginally more tolerant of defoliation than *B. gracilis*.

These results raise questions about the ability of greenhouse defoliation trials to reproduce field responses, especially since counter-intuitive outcomes are not unprecedented. Bock et al. (1995) found that alpine grasses from the Caucuses performed worse than grasses from Rocky Mountain alpine communities, though the field responses suggested that the Asian species were more grazing tolerant. Other greenhouse defoliation studies found few differences in response among very different species. *A. smithii* and *B. gracilis*, shortgrass steppe plants that I used as well, showed similar reductions in biomass with clipping for both species (Painter et al. 1989). Wilsey et al. (1997), comparing grasses from Yellowstone National Park, USA, the flooding pampa of Argentina, and the Serengetti, found no differences in aboveground performance, though Serengetti grasses experienced less reduction of belowground biomass following defoliation.

Why would grazing increasers, species known to be resistant to grazing under field conditions, be outperformed or equaled in the greenhouse by grazing decreasers? One possible explanation is that grazing tolerance, measured at the individual plant level, is less important than avoidance in determining the population level response of species to grazing in field settings. Anderson and Briske (1995) showed that replacement of a competitive dominant by a subordinate species was driven by selective herbivory, not differences in tolerance. Similarly, differences in competitive ability can have stronger effects on abundance than grazing tolerance (Hendon and Briske 2002). A second explanation is that differences between field and greenhouse conditions cause different outcomes following defoliation. A likely cause of such differences would be the low root-to-shoot ratios of potted plants grown in the greenhouse. In my experiment, the mean root:shoot ratio of *B. gracilis* control replicates was 1.3, whereas typical values in ungrazed shortgrass steppe range from 7 to 8.8 (Milchunas and Lauenroth 1989). This difference may have important implications for regrowth potential.

Anecdotal evidence for morphological plasticity

Morphological plasticity can create another form of grazing tolerance (McIntyre et al. 1999). For example, some grazing-adapted grasses adopt a prostrate growth habit in response to grazing (Hickey 1961). My analysis of avoidance traits did not include measurements of changes in plant growth form following defoliation. Field observations, however, suggest that Patagonian but not sagebrush grasses may possess such morphological plasticity. Concurrent with this study of plant traits, at each site I documented changes in vegetation with distance from stock watering points (Chapter 4). In semiarid ecosystems, water availability exerts a strong control on stock distribution, with heavier grazing close to water and light or no grazing in areas far from water (Lange 1969, Andrew 1988). In both Patagonia and sagebrush study areas, utilization decreased and cover of preferred forage grasses increased with increasing distance-from-water (Chapter 4). While leaf and flower height of the sagebrush dominant *A. spicatum* was relatively constant, heavily grazed individuals of an arid Patagonian dominant, *P. ligularis*, adopted a prostrate growth form. The coefficient of variation of leaf and flower height for 10 plants measured at each site ranged from 8-22% and 16-30%, respectively, for *A. spicatum*, and from 15-98% and 21-68% for *P. ligularis*. When grown in the greenhouse, differences between the "short" and "tall" forms of *P. ligularis* disappeared (pers. obs., M. Aguiar pers. comm.), suggesting that these forms do not represent distinct genotypes. This plasticity indicates a longer evolutionary history of grazing in Patagonia, but the differences in plant response are confounded by differences in grazing management--spring cattle grazing in sagebrush vs. year-round sheep grazing in

Patagonia. Given the importance of morphological plasticity as a grazing adaptation, this topic warrants further research.

Avoidance: evidence for an intense history of grazing in Patagonia

In contrast to the inconclusive results from the defoliation experiment, my analysis of avoidance traits provided evidence supporting the hypothesis that grazing has been a more important selection pressure in Patagonian steppe than in sagebrush steppe. Patagonian grasses, especially the dominants at the drier site, have tougher leaves that are lower in N and higher in fiber than leaves of sagebrush steppe grasses. Patagonian species are also shorter, though this difference is minimized when only dominants are considered. The ordination scores showed that shortgrass steppe grasses are more similar to the Patagonian species than the sagebrush steppe species in terms of avoidance traits, further evidence that the Patagonia species may have evolved under strong grazing pressure.

Although silica has been reported to function as a defense against grazing (McNaughton et al. 1985), I found that silica values, while generally low, were positively correlated in the ordination with measures of palatability, such as content of N and cell solubles. Higher silica in plants preferred by grazers, also observed in previous studies (Cid et al. 1990), suggests that silica is not an effective anti-herbivore defense.

To argue that the differences in traits are evidence for more intense grazing history in Patagonia assumes that tough, poor quality leaves are an effective defense against herbivores. Herbivores do, in fact, avoid plants that are difficult to digest (and decompose) in favor of their more palatable competitors (Grime et al. 1996). This type of avoidance is further enhanced by tough leaves that result in large fractions of standing dead leaves, which even large herbivores avoid (Cruz et al. 1998). The dominant *S. speciosa* at the dry Patagonia site retains four times more standing dead biomass (Soriano 1976) than *A. spicatum* at an arid sagebrush site (Rickard et al. 1988). Removing dead leaves at the end of the growing season on individual *P. ligularis* plants, the primary forage species at the same Patagonia site, tended to decrease live biomass relative to untreated controls in the following year, presumably due to defoliation (Adler, Oesterheld, and Sala, unpublished data). That the *Stipa* species and *P. ligularis* continue to dominate communities protected from grazing for over 40 years suggests that their dominance is not simply a result of recent livestock grazing.

Avoidance: alternative explanations

Although the differences in avoidance traits between Patagonian and sagebrush grasses are consistent with a more intense evolutionary history of grazing in Patagonia, alternative explanations for these differences must be considered. Grazing is not the only selection pressure that might favor tough leaves and short plants. That wind contributes more to aridity in Patagonia than in sagebrush steppe, where high summer temperatures are more important, could have important implications for plant structure. Steep leaf-angles help shield plants from excessive radiation in semiarid environments, at a cost of increased self-shading and reduced carbon gain (Villadares and Pugnaire 1999). In a windy environment, leaves would have to be proportionally stiffer to maintain the same position. The larger area of true aridity in Patagonia suggests another alternative explanation. As aridity increases, grass leaf width decreases and leaf-rolling becomes more common, allowing plants to lower water vapor conductance and reduce overheating (Redmann 1985). All the arid Patagonian dominants have tightly rolled leaves, contributing to their rigidity. In a study of phenotypic variation, Oliva et al (1993) found that *F. pallescens* growing in dry areas of Patagonia had shorter, tougher leaves than plants growing in more mesic environments. Although extremely dry areas occur in the sagebrush steppe, they may be too small to effectively isolate drought tolerant genotypes from surrounding conspecifics, preventing local adaptation. By this reasoning, we should be more likely to find grasses with tough leaves in the hotter deserts to the south of my sagebrush steppe study sites. In fact, populations of *S. speciosa* (syn. *Achnaetherum speciosum*), a dominant in arid Patagonia, exist in Nevada, but primarily on harsh sites (Young and Evans 1980).

Nitrogen limitation offers a better environmental explanation for low forage quality in arid Patagonia. The soils at my arid Patagonian field site are extremely coarse, with sand content over 90%, and, regionally, sandy soils are more common in Patagonia than in the sagebrush step (Chapter 2). Coarse soils accumulate less N than finer textured soils because of higher N mineralization rates but lower stabilization of N through adsorption and aggregation onto clays (Schimel 1985a,b, Aguilar et al. 1988, Aguilar and Heil 1988). Indeed, arid Patagonian soils contained much less total N than soils from my arid sagebrush study area, despite similar levels of aboveground production (Chapter 4). N concentrations in bare ground at the arid Patagonian site were less than 0.05%. Low N availability would explain the low N content in grass tissue. In contrast, soils at the "wet" Patagonian site are not as coarse, have total soil N similar to sites in sagebrush steppe (Chapter 4), and support grasses with higher N content.

Finally, we cannot ignore the possibility that the tough leaves of Patagonian grasses are a legacy of evolutionary processes much farther in their past. Grasses throughout the semiarid temperate environments of South America are notably tough. Díaz et al. (2001) found that plants from the mountains of central Argentina had leaves with higher tensile strength than plants from Israel, which also has a long evolutionary history of grazing. In the central Andes, extending from northern Argentina into Ecuador, livestock avoid large tussock grasses with fibrous leaves such as *Stipa ichu* (Ellenburg 1979, Adler and Morales 1999). The similarity of Patagonian and Andean species is not coincidental; the Patagonian flora was derived primarily from Andean sources (Solbrig 1973). Many of the dominant species of the sagebrush steppe, in contrast, have Holarctic origins (Daubenmire 1975, Leopold and Denton 1987). Perhaps the high elevation environment of the central Andes, characterized by intense radiation, imposed selection pressures that continue to constrain plant structure. Unfortunately, while it is known that most South American grasses immigrated from Eurasia through North America (Soreng 1990), the phylogenetic history of the Pooideae, which includes *Poa*, *Stipa*, and *Festuca*, is very poorly understood (Grass phylogeny working group, 2001).

Implications for domestic livestock grazing

Regardless of their origin, differences in plant traits of grasses from Patagonia and the sagebrush steppe suggest that the introduction of domestic livestock should have different effects in these ecosystems. The presence of both palatable and extremely unpalatable grasses in arid Patagonia means that grazing should cause large changes in relative abundance within this functional group, but few changes in overall grass abundance. Field studies provide evidence of this contrast. Grazing at the dry Patagonia site causes an increase in the unpalatable *Stipa* species, and a decrease in the more palatable perennial grasses, but little change in the overall abundance of perennial grasses (Soriano 1976, Chapter 4). In the sagebrush steppe, grazing causes dramatic decreases in the abundance of perennial grasses (Mueggler 1950, Laycock 1967, Chapter 4). More humid communities in Patagonia respond more similarly to the sagebrush steppe, with decreases in overall grass abundance (León and Aguiar 1985, Chapter 4). The different responses at the wet and dry Patagonian sites should be expected given their difference in forage quality.

The second implication of poor forage quality in Patagonia has to do with its negative effects on secondary production. When the crude protein content of grasses falls below 7-10 %, ruminants can experience bulk limitation, meaning that the rate of passage of material through the gut slows enough to cause a decrease in voluntary intake rate (reviewed in Allison 1985). Assuming that crude protein can be estimated as 6.25 times N concentration, the N threshold is 1.1 –1.6%. The dominant species at the dry Patagonia site all fell below this threshold, with N content ranging from 0.72 to 0.77%, and the mean N content for all species at the site was 0.93% (Table 3.3). N content in senescent leaves of the dominants from this site ranged from 0.29 to 0.34%. These surprisingly low N content values were confirmed by similar values in the samples collected the previous year (not shown). As evidence of the impact of low N forage on livestock, Golluscio et al. (1998) showed that urea supplementation increased forage digestibility and intake rates of pregnant ewes on dry Patagonian steppe. N content was slightly higher for species at the wet Patagonia site, but much higher at the sagebrush steppe dry and wet sites with means for dominants of 1.27 and 1.40% respectively.

These values match published data for the same species collected near the end of the growing season (Murray et al. 1978, Ganskopp and Bohnert 1998).

If poor forage quality is limited to only a few species, or subordinate species, it is unlikely to affect intake rates. But when the dominant plant species at a site all have low crude protein content, and the availability of higher quality species is limited, as at the dry Patagonia site, forage quality may exercise a strong influence on herbivore populations. Again, field data support this expectation: consumption and utilization were lower in Patagonian steppe than sagebrush steppe (Chapter 4). Decreases in lambing rates observed with increasing stocking rates (Anchorena and Cingolani 1999) further support the hypothesis that low forage quality limits herbivore carrying capacity. Ironically, the same plant traits that appear to limit livestock production may reduce the ecosystem's vulnerability to grazing impacts.

Status of the evolutionary history of grazing concept

The evolutionary history of grazing concept has influenced grazing research for more than two decades (Stebbins 1981, Mack and Thompson 1982, Milchunas et al. 1988). Is it still useful? After all, if our objective is to predict the current response of plant communities to grazing, then all we need is information on plant traits, as recent work including this dissertation demonstrates. However, we can never know if we have measured the critical plant functional traits, nor do we have data on plant traits in all ecosystems and communities where grazing is an important land-use. Furthermore, whether predictions based on plant traits apply to grazing effects on other taxa or on ecosystem properties such as nitrogen cycling is uncertain. The evolutionary history concept can serve as a qualitative predictor to patch these gaps in knowledge. But more importantly, even if plant traits can predict ecosystem responses to present grazing, they cannot explain the great variability among ecosystems. Plant traits themselves are legacies of abiotic and biotic selection pressures, including the evolutionary history of grazing. Understanding why different plant traits evolved in different ecosystems will require careful consideration of the role of evolutionary history of grazing and its interactions with abiotic factors. My results suggest that these efforts should focus on traits related to grazing avoidance, rather than tolerance, and on abiotic factors related to N limitation, primarily soils.

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Table 3.1. List of measured traits with their units and abbreviations (used on the ordination diagrams).

Code	Trait	Units
leaf ht	Leaf height	cm
flwr ht	Flower height	cm
leaf wi1	Leaf width	mm
leaf wi2	Leaf thickness	mm
blade	Length of leaf blade	cm
sheath	Length of leaf sheath	cm
force	Leaf tensile strength	Newtons (kg m^{-s} s^{-2})
vegrepr	Vegetative reproduction	categorical (yes, no)
cellsols	Cell solubles	g/g
hemicell	Hemicellulose	g/g
cellul	Cellulose	g/g
lignin	Lignin	g/g
ash	Ash	g/g
C	Carbon	%
N	Nitrogen	%
Si	Silica	mg/kg
P	Phosphorus	mg/kg

Table 3.2. Defoliation response (estimated mean production of defoliated treatments divided by estimated mean production of control treatments) for the greenhouse experiment.

Region	Species	Aboveground clipped/control	Belowground clipped/control
Shortgrass	*A. smithii*	0.27	0.12
Shortgrass	*B. gracilis*	0.41	0.36
Sagebrush	*A. spicatum*	0.45	0.35
Sagebrush	*F. idahoensis*	0.47	0.38
Sagebrush	*P. secunda*	0.60	0.54
Patagonia	*F. pallescens*	0.60	0.48
Patagonia	*P. ligularis*	0.61	0.39

Table 3.3. List of species from each site and values for selected traits (leaf and flower height in cm, tensile strength in Newtons, Nitrogen in %). Dominant species are shown in bold.

Region	Precipitation	Spp. code	Species name	Leaf height	Flower height	Tensile strength	*N*
Sagebrush	"dry"	g1	***Agropyron spicatum***	37	59	0.95	1.04
	(175 mm)	g2	*Orizhopsis hymenoides*	33	52	0.96	1.43
		g3	*Poa cusickii*	18	42	0.23	1.67
		g4	***Poa secunda***	6	31	0.22	1.52
		g5	*Sitanion hystrix*	16	29	1.20	1.73
		g6	*Stipa comata*	28	60	0.91	1.89
		g7	***Stipa thurberiana***	26	39	0.66	1.26
			Mean (all species)	23	44	0.73	1.51
			Mean (dominants)	23	43	0.61	1.27
Sagebrush	"wet"	G1	***Agropyron spicatum***	35	46	0.68	1.46
	(300 mm)	G2	*Carex filifolia*	20	21	0.52	1.68
		G3	***Festuca idahoensis***	25	36	0.77	1.09
		G4	*Poa juncifolia*	29	46	1.25	1.22
		G5	*Poa secunda*	7	29	0.36	1.65
		G6	*Stipa nelsonii*	28	41	0.73	1.69
		G7	***Stipa comata***	21	34	0.72	1.63
			Mean (all species)	23	36	0.72	1.49
			Mean (dominants)	27	39	0.72	1.40
Patagonia	"dry"	p1	*Bromus pictus*	9	19	0.84	1.15
	(154 mm)	p2	*Bromus setifolius*	11	17	0.90	1.05
		p3	*Carex andina*	5	1	2.56	0.76
		p4	*Festuca argentina*	28	51	3.76	1.11
		p5	*Hordeum comossum*	10	20	0.37	1.22
		p6	*Poa lanigunosa*	9	19	1.51	0.71
		p7	***Poa ligularis***	18	22	4.95	0.73
		p8	***Stipa humilis***	17	23	1.31	0.77
		p9	*Stipa psylantha*	19	35	1.75	1.07
		p10	***Stipa speciosa***	19	29	1.84	0.72
			Mean (all species)	15	24	1.98	0.93
			Mean (dominants)	18	25	2.70	0.74
Patagonia	"wet"	P1	*Bromus pictus*	12	27	1.07	1.34
	(400 mm)	P2	*Carex andina*	3	1	0.50	0.97
		P3	***Festuca magellanica***	6	21	0.59	0.77
		P4	***Festuca pallescens***	25	48	1.25	0.98
		P5	*Hordeum comossum*	13	27	0.58	1.54
		P6	*Koeleria grisebachii*	5	20	0.60	1.32
		P7	*Luzula chilensis*	6	29	0.46	1.14
		P8	***Poa ligularis***	16	31	2.02	0.90
		P9	*Rhytidosperma picta*	5	4	0.35	1.16
			Mean (all species)	10	23	0.82	1.13
			Mean (dominants)	16	33	1.29	0.88
Shortgrass	(310 mm)	S1	***Agropyron smithii***	28	58	2.42	1.39
		S2	*Aristida longifolia*	11	21	0.82	1.14
		S3	***Bouteloua gracilis***	8	23	0.33	1.34

S4	***Buchlöe dactyloides***	6	9	0.25	1.35
S5	*Carex eleocharis*	18	22	0.60	1.75
S6	*Carex filifolia*	15	18	0.46	1.54
S7	*Sitanion hystrix*	15	25	1.11	1.83
S8	*Sporobolus cryptandra*	27	58	1.24	1.23
S9	*Stipa comata*	30	61	1.15	1.48
	Mean (all species)	17	33	0.93	1.46
	Mean (dominants)	14	30	1.00	1.37

Table 3.4. Results of two-way ANOVA on PCA axis 1 and 2 scores, using all species and only dominant species. SGS plants were excluded from this ordination.

PCA axis 1, all species

Source	Sum of squares	df	F	p
Model	3.067	3	2.028	.132
Intercept	0.069	1	0.136	.715
Region	2.515	1	4.987	.033
Precipitation	0.0004	1	0.001	.978
Region*Ppt	0.474	1	0.941	.340
Error	14.623	29		

PCA axis 1, dominant species

Source	Sum of squares	df	F	p
Model	4.651	3	13.891	.002
Intercept	1.218	1	10.915	.011
Region	3.397	1	30.442	.001
Precipitation	0.381	1	3.411	.102
Region*Ppt	0.873	1	7.820	.023
Error	0.893	8		

PCA axis 2, all species

Source	Sum of squares	df	F	p
Model	5.479	3	5.018	.006
Intercept	0.119	1	0.327	.572
Region	5.439	1	14.945	.001
Precipitation	0.063	1	0.174	.679
Region*Ppt	0.0007	1	0.002	.965
Error	10.554	29		

PCA axis 2, dominant species

Source	Sum of squares	df	F	p
Model	0.910	3	0.643	.609
Intercept	0.581	1	1.231	.299
Region	0.811	1	1.719	.226
Precipitation	0.063	1	0.134	.723
Region*Ppt	0.036	1	0.075	.790
Error	3.774	8		

Table 3.5. Results of one-way ANOVA on PCA axis 1 and 2 scores, using all species and only dominant species. SGS plants were included in this ordination.

PCA axis 1, all species				
Source	Sum of squares	df	F	p
Between groups	1.825	4	0.904	.471
Within groups	18.945	37		
Total	20.798			
PCA axis 1, dominant species				
Source	Sum of squares	df	F	p
Between groups	3.194	4	2.693	.075
Within groups	2.695	10		
Total	5.889			
PCA axis 2, all species				
Source	Sum of squares	df	F	p
Between groups	7.363	4	5.334	.002
Within groups	12.769	37		
Total	20.133			
PCA axis 2, dominant species				
Source	Sum of squares	df	F	p
Between groups	2.660	4	2.012	.169
Within groups	3.306	10		
Total	5.966			

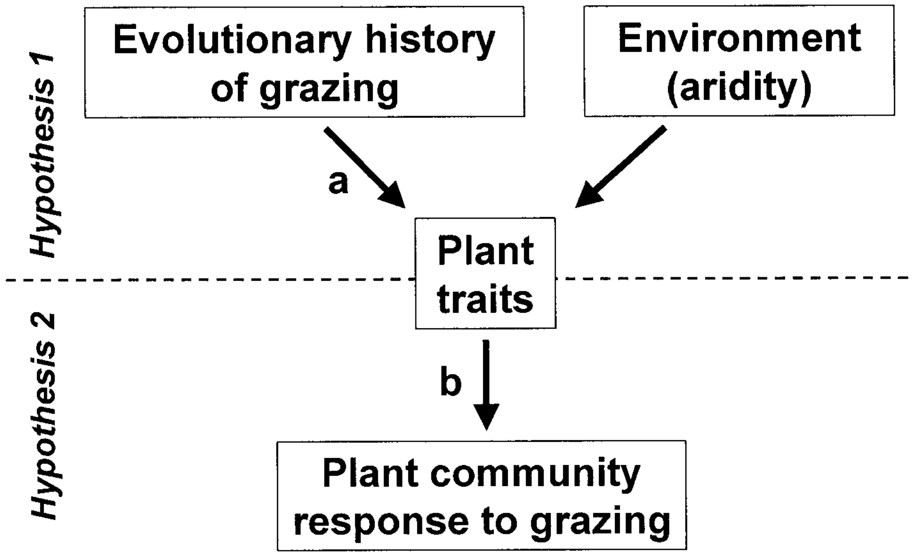

Fig. 3.1. Restatement of the Milchunas et al. (1988) model, making explicit the role of plant traits. In this chapter, I use information on plant traits to make inferences about evolutionary history of grazing, moving in reverse on the arrow labeled "a," and also to generate predictions about plant community responses to grazing, as indicated by arrow "b."

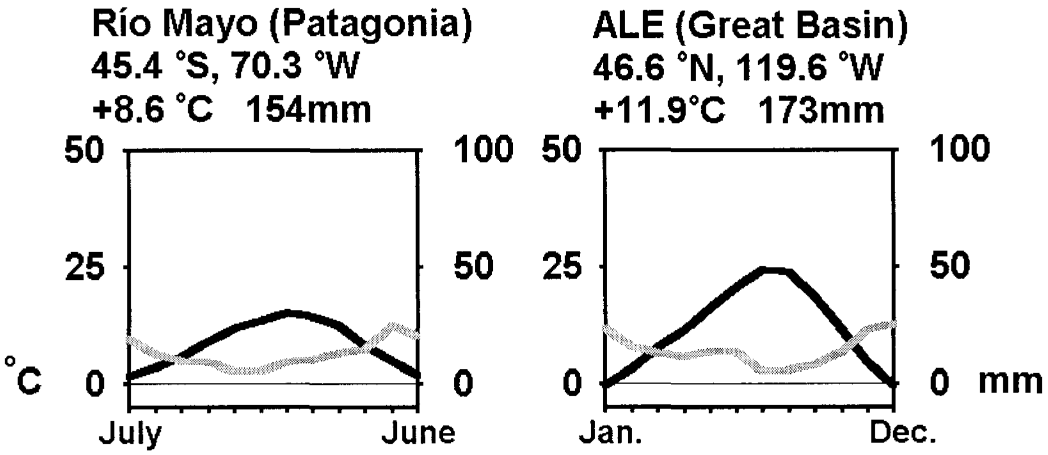

Fig. 3.2. Mean monthly precipitation and temperature for dry sites in Patagonia (Beltrán 1997) and the sagebrush steppe (Hoitink et al. 1999).

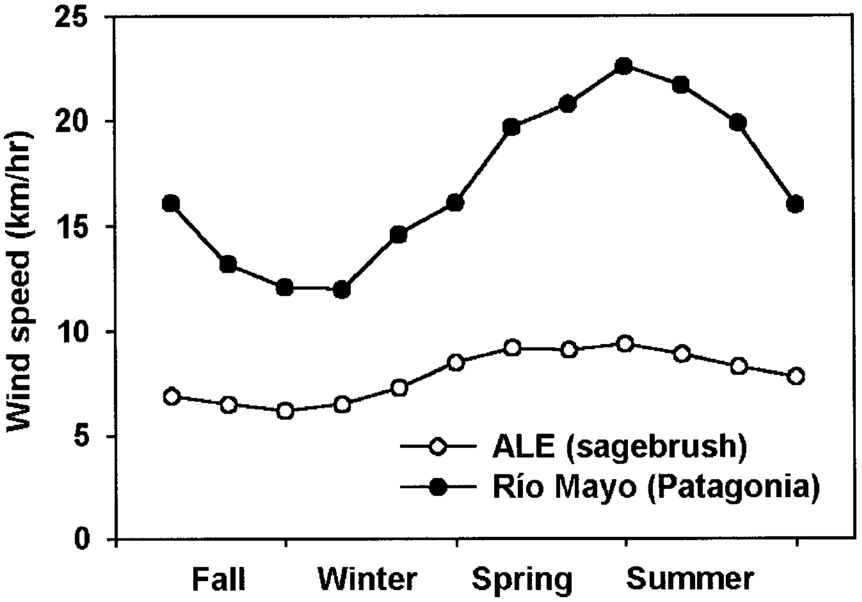

Fig. 3.3. Mean monthly wind speeds at 2 m above the ground surface in Patagonian steppe (Beltrán 1997) and sagebrush steppe (estimated from Hoitink et al. 1999).

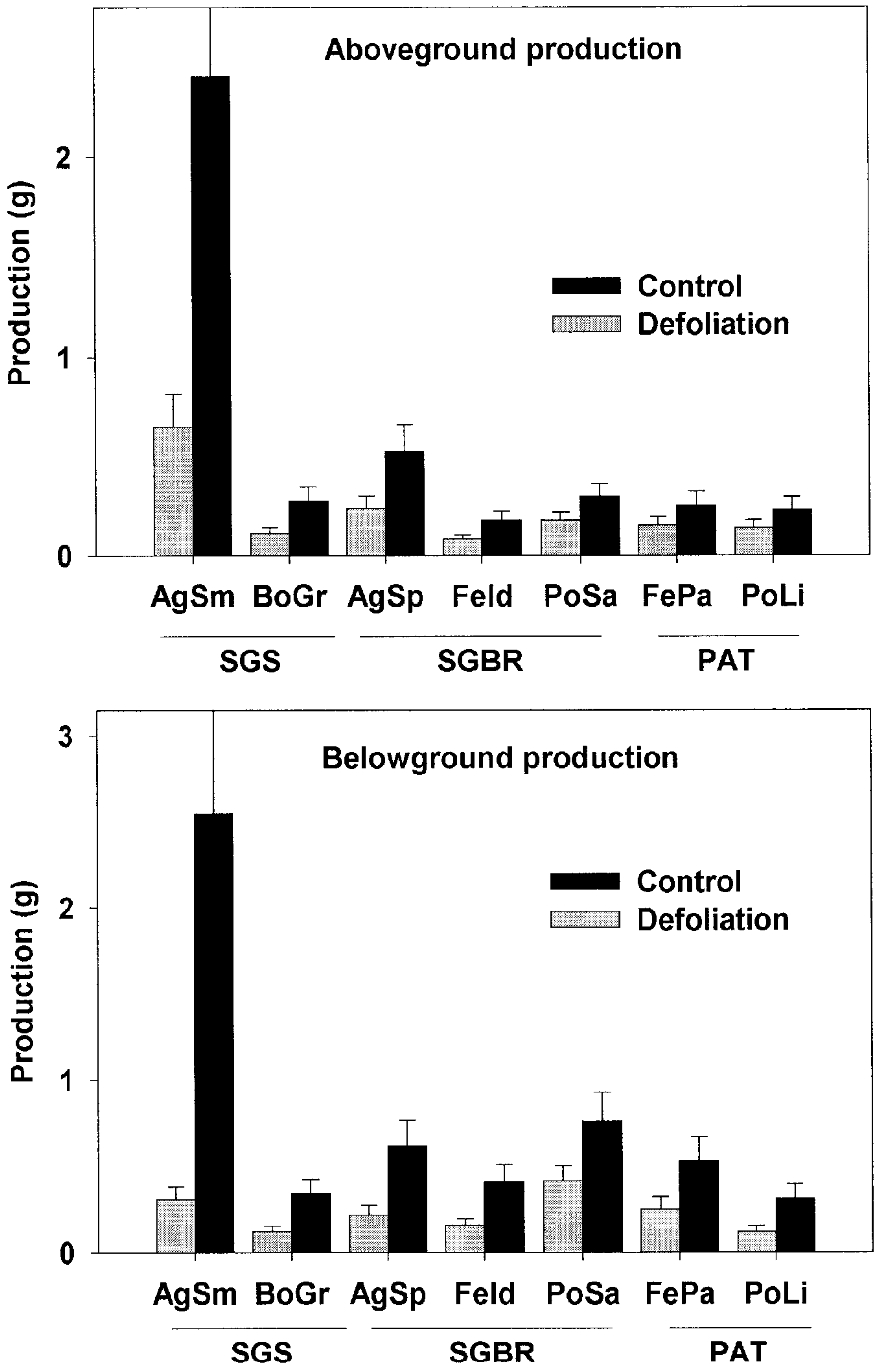

Fig. 3.4. Results of the defoliation experiment. Shown are least squares means and standard errors. Four letter species codes refer to the first two letters of the genus and specific epithet (full names listed in Table 3.3).

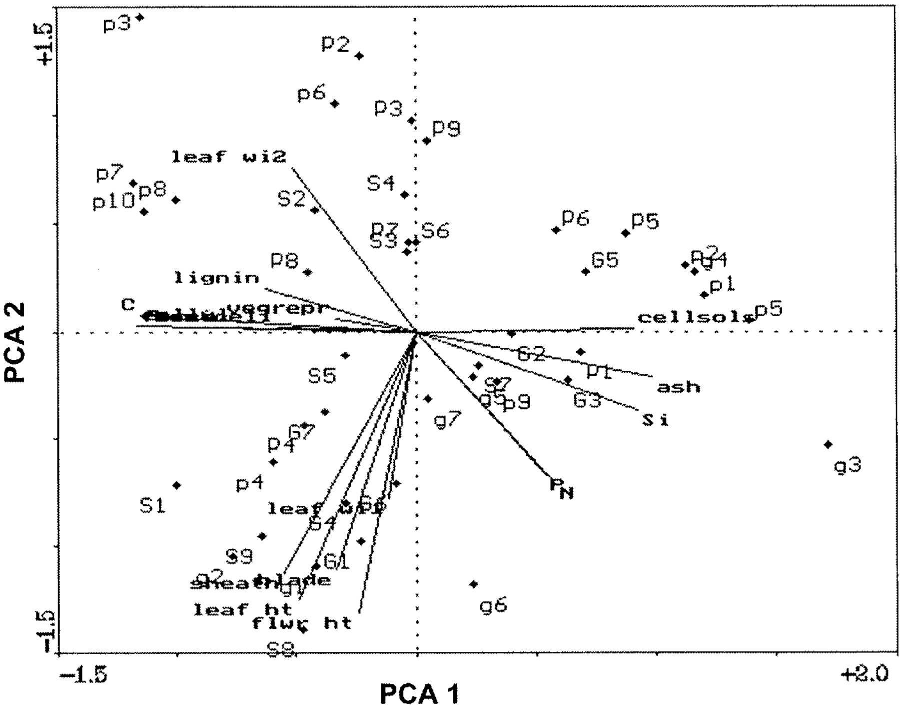

Fig. 3.5. Results from the PCA: Solid lines show the loading of traits (trait abbreviations listed in Table 3.1), and points show the scores of individual species from each site (codes are defined in Table 3.3).

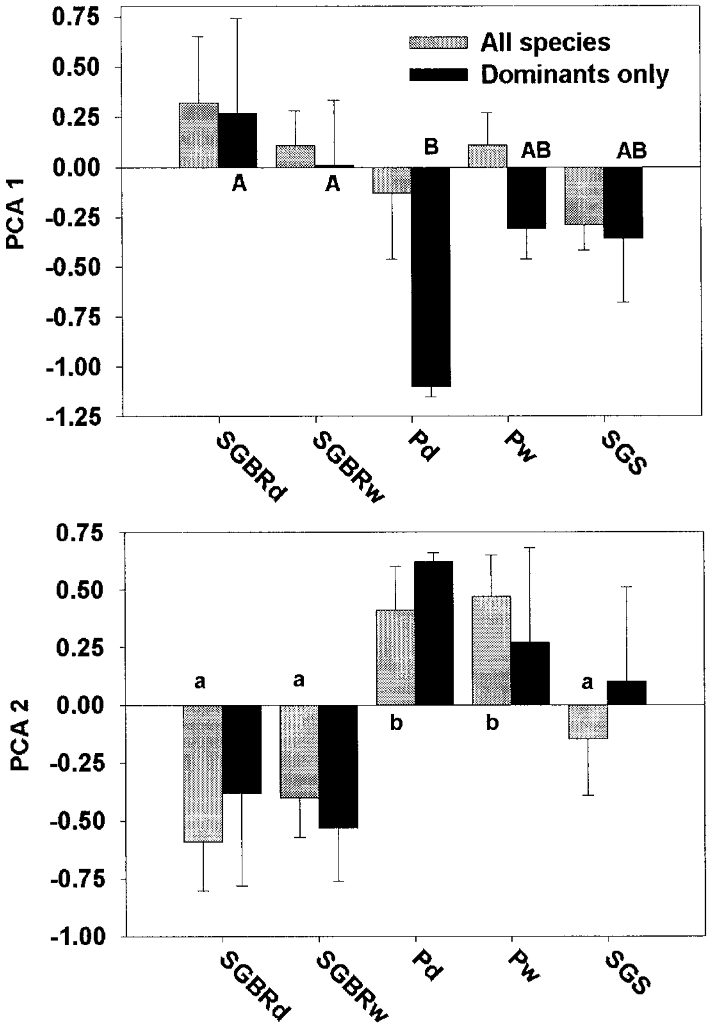

Fig. 3.6. Mean scores by site for all species and dominant species on PCA axes 1 (above) and 2 (below). "SGBRd" and "SGBRw" = sagebrush steppe dry and wet, "Pd" and "Pw" = Patagonian steppe dry and wet, "SGS' = shortgrass steppe. Bars sharing a letter are not significantly different (post-hoc LSD test, α<.05, results shown only for significant ANOVA models). Capital letters refer to dominant species scores, lower case to all species means.

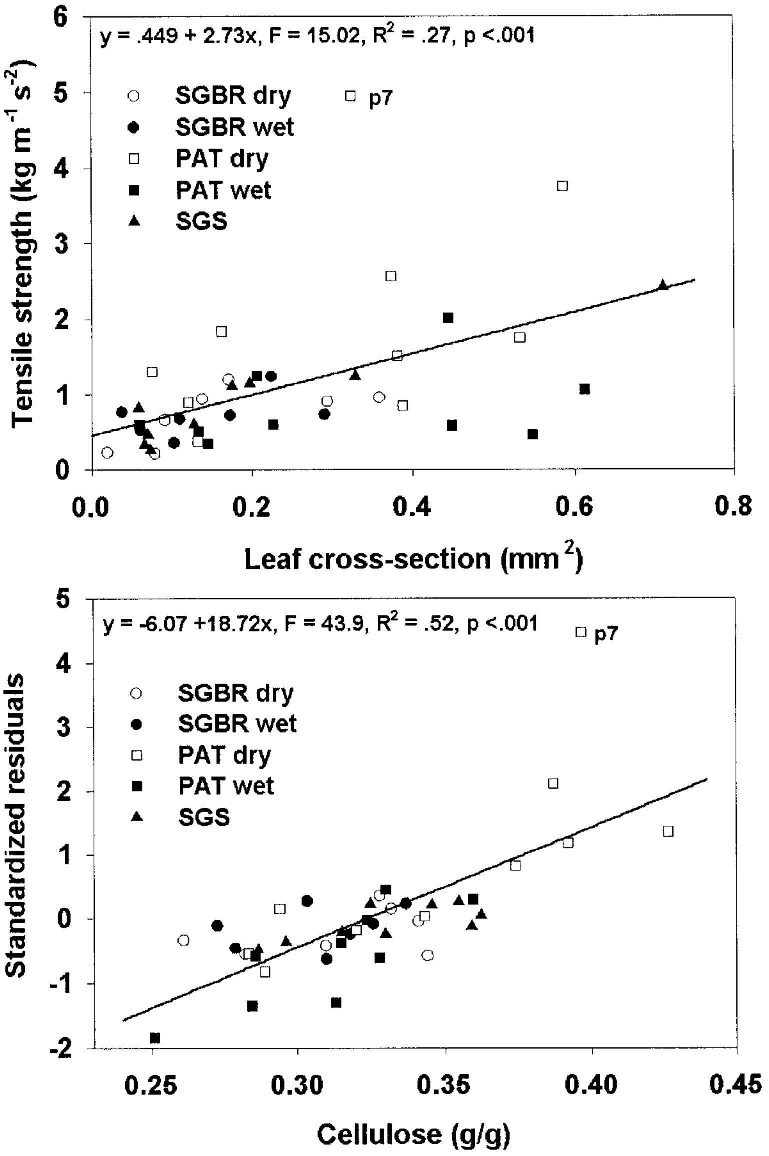

Fig. 3.7. Leaf cross-sectional area explains some variation in leaf tensile strength (upper panel), and the remaining variation is best explained by cellulose content (lower panel).

CHAPTER 4: COMPARISON OF LIVESTOCK GRAZING EFFECTS ON VEGETATION AND SOILS IN SAGEBRUSH STEPPE, USA AND PATAGONIAN STEPPE, ARGENTINA

ABSTRACT

Grazing by domestic livestock has dramatic effects on vegetation in some ecosystems, but only subtle effects in others. The effect of grazing is determined by the frequency and degree of plant adaptations to grazing, which, according to the Milchunas et al. (1988) conceptual model, are influenced by 1) precipitation and 2) the evolutionary history of grazing. To test the predictive power of evolutionary history, I compared vegetation response to grazing in the sagebrush steppe of North American (SGBR) and the Patagonian steppe of South American (PAT). These regions have very similar climates, but evidence suggests a shorter evolutionary history of grazing in SGBR than PAT. Therefore, the Milchunas model predicts that SGBR will be more sensitive to grazing than PAT.

In both regions, I sampled consumption and utilization, primary production, species composition, and total soil C and N across gradients of precipitation and distance from water, a proxy for historical grazing pressure. Direct and indirect measures of grazing intensity generally declined as expected with distance from water, but the highest values of grazing intensity often occurred at sites at intermediate distances. Both consumption and utilization, measured by direct harvest, were higher in SGBR than PAT.

This difference in grazing pressure led to corresponding differences in grazing response that were generally consistent with the prediction of the Milchunas model. Abundance of perennial grasses increased with distance from water in SGBR and subhumid PAT, but not in arid PAT, while shrub production decreased with distance in SGBR but not PAT. Likewise, grazing caused significant decreases in total production in SGBR but not PAT. Grazing variables explained much less variation in species composition in arid PAT (43%) than in any other study area (59-74%). Plant species richness at the 1 m^2 scale showed a weak unimodal trend across grazing intensity gradients in both regions, but was unaffected by grazing at the site scale. Total richness increased more steeply across the precipitation gradient in SGBR than PAT, while non-native species number increased more dramatically across the PAT precipitation gradient.

The differences in grazing pressure between regions, the putative cause for contrasts in the effect of grazing on vegetation, could be a result of the low forage quality of dominant PAT bunchgrasses. The low N content and high C:N ratios of these plants may be caused, in turn, by nitrogen limitation arising from the extremely coarse Patagonian soils, especially at the arid study area. Data showing much lower total soil C and N in arid PAT compared to arid SGBR support this hypothesis. Potential N limitation may explain why Patagonian plants evolved defense rather than tolerance to grazing. Although well-defended plants limit livestock production, they make the ecosystem more resistant to overgrazing than one dominated by poorly defended plants, such as the sagebrush steppe.

INTRODUCTION

Grazing by domestic livestock has dramatic effects on vegetation in some ecosystems but only subtle effects in others (Milchunas and Lauenroth 1993). To explain this variability in grazing impacts, recent work has focused on plant functional traits conferring tolerance and resistance to grazing (McIntyre et al.1999, Díaz et al. 2001). In ecosystems where dominant plant species possess such grazing adaptations or ex-aptations (Gould and Lewontin 1979), vegetation should be less sensitive to grazing than in systems where grazing adaptations are rare. One factor that determines whether plants develop adaptations to grazing is moisture, because adaptations to aridity such as belowground meristems and short-stature also confer resistance to grazing (Coughenour 1985). The evolutionary history of grazing, meaning selection pressures imposed by native grazers over ecologically relevant time scales, is a second factor influencing the development of grazing adaptations (Stebbins 1981, Mack and Thompson 1982). Milchunas et al. (1988) constructed a conceptual model that predicts the effects of grazing on plant communities as a function of these two independent factors. Therefore, testing the ability of evolutionary history of grazing to explain variability in grazing impacts requires a comparison of ecosystems with independent evolutionary histories but similar moisture, or climatic, regimes.

The comparison of the shortgrass steppe and sagebrush steppe of North America provided much of the initial evidence for the importance of evolutionary grazing history (Mack and Thompson 1982, Milchunas et al. 1988). The shortgrass steppe, east of the Rocky Mountains, with its history of intense grazing by bison, is extremely grazing tolerant (Milchunas et al. 1989) while the sagebrush steppe, on the west side of the continental divide, lacked dense herds of native grazers (Daubenmire 1970, Mack and Thompson 1982, Lyman and Wolverton 2002) and is sensitive to livestock grazing (reviewed in Miller et al. 1994). But this comparison is confounded by differences in climate, the second determinant of plant adaptations to grazing. While mean annual precipitation in some areas of these two systems is comparable, precipitations falls mainly in winter in the sagebrush steppe, and in spring and summer in the shortgrass steppe. To evaluate the importance of evolutionary history, a more appropriate comparison would pair the sagebrush steppe with another arid to semiarid region characterized by winter precipitation, but one with a longer evolutionary history of grazing. The Patagonian steppe of southern Argentina meets these criteria.

The sagebrush steppe and Patagonian steppe are well matched with respect to abiotic factors. Both regions, located near 45° latitude (Fig. 4.1), occupy rain shadow deserts created by the uplift of the Cascades and Andes during the Pliocene (Solbrig 1973, Wolfe 1969). Pleistocene glaciations and accompanying alluvial and aeolian deposition created soils from similar granitic and basaltic parent materials (Mapa Geológico de la República Argentina 1997, Jensen et al. 1997). Current climate in both regions is characterized by cool winters and warm, dry summers, with precipitation concentrated in fall through spring. Based on an analysis of mean annual temperature, precipitation, and precipitation timing, Paruelo et al. (1995) identified areas of the sagebrush steppe and Patagonian steppe as an example of strong regional climatic similarity. Vegetation reflects the climatic similarity: shrubs and caespitose C_3 bunchgrasses dominate plant communities in both regions, with grasses increasing in importance in the coolest, wettest areas and shrubs in the driest and warmest (Küchler

1964, León et al. 1998; Fig. 4.1). A satellite derived vegetation index demonstrated convergence in the structure and function of sagebrush and Patagonian steppe (Paruelo et al. 1998).

While the climatic similarity of these two regions is firmly supported by data, our understanding of the difference in their evolutionary grazing histories relies on indirect evidence. In fact, Milchunas et al. (1988) used both systems as examples of semiarid regions with short evolutionary histories of grazing. 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), however, suggest that Patagonia may have a longer history of grazing than the sagebrush steppe. Below, I present archeological evidence and review an analysis of plant functional traits that support this alternative view.

Archeological and historical evidence from the sagebrush steppe makes a strong case for the absence of dense populations of ungulates, at least during the late Holocene. Based on remains found in human archeological sites, 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). Likewise, elk were scarce relative to areas east of the continental divide (Dixon and Lyman 1996). Hunting records from the Lewis and Clark expedition also illustrate the severity of this "game sink" (Lyman and Wolverton 2002). Mack and Thompson (1982) noted the presence of biological soil crusts and the absence of rhizomatous grasses and dung beetles in sagebrush steppe as further evidence of a lack of coevolution with grazers. The cause of such low ungulate densities is most likely a combination of low herbaceous production, occasional severe winters, barriers to recolonization from the east following local extinctions, and human hunting pressure (Daubenmire 1985, van Vuren 1987, Lyman and Wolverton 2002).

The available information on ungulate populations from Patagonia, in contrast, suggests high densities until European colonization. Although Markgraf (1985) showed that late-Pleistocene extinctions decimated the South American megafauna, as they did in North America (Brown and Lomolino 1998), native camelids such as the guanaco (*Lama guanicöe*) survived. Indigenous cultures in Patagonia depended on the guanaco for food and materials for clothing and shelter (Franklin 1981). Despite this hunting pressure, guanaco were still numerous enough in the early 19th century that sheep ranchers called for the eradication of the "pest" (Franklin 1981). As late as the 1970's, 400,000 guanaco hides were exported from Buenos Aires (Franklin 1981). Guanaco currently survive at high densities in nature reserves, and their inverse relationship with sheep abundance and similarity in diet suggest that their decline in unprotected areas may be caused as much by competition as hunting pressure (Baldi et al. 2001).

My comparison of functional traits in common grasses of each region (chapter 3) further supports the case for a longer evolutionary history of grazing in Patagonia. The Patagonian grasses tended to be shorter than the sagebrush steppe grasses, although this difference weakened if only the dominants were considered. More importantly, the Patagonian grasses, especially those from the driest sites, were tougher, lower in nitrogen, and had higher C:N ratios and concentrations of fiber. These differences were strengthened when only the dominants were considered. Low stature and unpalatable tissue may have evolved as defenses against herbivory. However, alternative explanations based on contrasting selection pressures created by subtle differences in the abiotic environment, such as the higher winds or coarser soils common in Patagonia, cannot be rejected. Regardless of the causes of such differences in forage quality, they influence stocking rates of domestic livestock and, in turn, impacts on plant communities.

If sagebrush steppe had a less intense evolutionary history of grazing than Patagonian steppe, then the Milchunas et al. model would predict that domestic livestock grazing would have larger effects on sagebrush steppe structure and function. Effects of grazing on sagebrush steppe are well documented and often dramatic. Spring (growing season) grazing by both sheep (Mueggler 1950, Laycock 1967, Bork et al. 1998) and cattle (Daubenmire 1940, Pond 1960, Pearson 1965, Rickard et al. 1975, Brotherson and Brotherson 1981) reduced the abundance of perennial grasses and in some cases increased the abundance of shrubs, while fall grazing either had no effect or a positive effect on grass abundance (Mueggler 1950, Laycock 1967, Bork et al. 1998). Clipping experiments in the field produced similar results. Spring clipping had strong negative effects on many bunchgrass species (Daubenmire 1940, Blaisdell 1949, Caldwell et al. 1981, Ganskopp 1988), and the native *Agropyron spicatum* replaced defoliated tissue less rapidly than the introduced *Agropyron desertorum* (Caldwell et al. 1981). Following removal of livestock, perennial grass abundances rebounded in some study areas (Sneva et al. 1984, Rose 1994) but not where the invasive annual *Bromus tectorum* had established (West et al. 1984). However, in one long-term trial, moderate season-long grazing by cattle did not produce significant differences in plant composition relative to ungrazed exclosures (Sneva et al. 1984). This apparent contradiction with previous results highlights a lack of understanding of how differences in grazing intensity affect sagebrush steppe (Miller et al. 1994).

Research on grazing in Patagonian steppe suggests both similarities and differences to sagebrush steppe. The livestock industry in Patagonia is composed primarily of sheep, with some cattle in the most productive areas (Soriano 1983), contrasting with the current dominance of cattle in the sagebrush steppe. In the Subandean district, the wettest part of the Patagonian steppe (León et al. 1998), grazing reduces cover of the dominant, palatable bunchgrass *Festuca pallescens*, and tends to increase the cover of bare ground and the shrub *Mulinum spinossum* (León and Aguiar 1985, Bertiller 1994, Bertiller 1995). Grazing increases the productivity of *F. pallescens* early in the growing season, but decreases it during the reproductive phase, leading to an overall decrease in aboveground production (Bertiller and DeFossé 1990). In the more arid Occidental District, where unpalatable *Stipa* species are co-dominant with the palatable *Poa ligularis*, grazing effects tend to be subtle: the primary change is a decrease in *P. ligularis* abundance (Soriano 1976) and increases in the abundance of *Stipa* species and shrubs (Soriano 1983). However, grazed areas had slightly higher total aboveground production than long-term ungrazed areas (Soriano 1983). This result seems to contradict claims of widespread desertification in the Patagonian steppe caused by overgrazing (Soriano 1983). Strong declines in livestock production through much of the 20th century, however, do provide evidence of desertification (Soriano and Paruelo 1990, Paruelo and Sala 1992a). Severe degradation of spatially limited wet meadows, which provide a disproportionate amount of the annual forage (Somlo et al. 1992), could explain both declines in secondary production and the absence of changes in production in arid upland vegetation.

My objective was to use the sagebrush steppe-Patagonian steppe comparison to test the importance of evolutionary grazing history as a determinant of ecosystem response to introduced livestock grazing. At arid, semiarid, and subhumid study areas within each region, I established sampling sites across gradients of contemporary grazing impacts in order to measure four sets of variables: consumption and utilization by livestock, aboveground primary production, plant species composition, and soil organic matter. By comparing the degree of change in vegetation and soils caused by grazing, I addressed the question, are differences in the effects of grazing consistent with a longer evolutionary history of grazing in the Patagonian steppe?

METHODS

Description of study areas

In both the sagebrush and Patagonian steppe, I selected three study areas that span the regional precipitation gradients (Fig. 4.1, Table 4.1). I focused on the portion of the sagebrush steppe (SGBR) within the Columbia Basin of eastern WA, one of the only parts of the SGBR with locations as arid as those in Patagonia. I used two criteria in selecting study areas. First, I required large areas of native vegetation, mostly free of invasion. Second, I required current grazing management consistent with historical management (see below), and pastures large enough to create strong gradients in grazing intensity.

In the sagebrush steppe (SGBR), the arid study area is located at Wanapum State Park near Vantage, WA, with a mean annual precipitation of approximately 170 mm (National Climatic Data Center). Vegetation belongs to the *Artemisia tridentata-Agropyron spicatum* association (Daubenmire 1970), though lithosols, dominated by *Eriogonum* spp. and *Poa secunda,* are common. The semiarid SGBR study area, with roughly 250 mm mean annual precipitation (Daly et al. 1994), is located in higher elevations to the west of the arid study area, on a private ranch just south of Ellensburg, WA. The *A. tridentata-A. spicatum* association is dominant at this study area as well, though *Festuca idahoensis* and *A. tripartita* occur on the highest, most shaded sites. The wettest SGBR study area, receiving at least 300 mm per year (Daly et al. 1994), sits just below the boundary between semiarid and subhumid systems as defined by Bailey (1979), but I will refer to it as the subhumid study area for clarity. This study area is located on state land in northern Douglas County, WA, just west of Grand Coulee. Vegetation belongs to the *A. tripartita – F. idahoensis* association (Daubenmire 1970). Unlike the other two SGBR study areas, the subhumid site was periodically affected by glaciation during the Pleistocene (Daubenmire 1970). I refer collectively to the vegetation of these three study areas as sagebrush steppe (SGBR). Botanical nomenclature follows Hitchcock and Cronquist (1973).

The arid study area in the Patagonian steppe (PAT) is the Río Mayo Experimental Station of the Instituto Nacional de Tecnología Agropecuaria located in central Chubut province. Mean annual precipitation is 154 mm, but recent observations using an automatic rain gauge suggest that the long-term record, based on manual observations, may underestimate precipitation by up to 30 mm per year (Beltrán 1997). The dominant shrub is *Mulinum spinossum*, and the dominant grasses are *Stipa speciosa*, *Stipa humilis*, and *Poa ligularis*, representative of the Occidental District vegetation type (León et al. 1998). The semiarid study area is located on the Estancia Valle Huemules, just west of the town of Lago Blanco, in western Chubut province. Mean annual precipitation is approximately 250 mm (Bertiller et al. 1995), and vegetation, dominated by *M. spinossum*, *P. ligularis*, and *Festuca pallescens*, is characteristic of the Subandean District (León et al. 1998), though *Stipa* spp. are still common on some sites. The subhumid Patagonian study area sits just east of the Chilean border, also part of the Estancia Valle Huemules. Mean annual precipitation is roughly 400 mm (local records, Bertiller et al. 1995), and vegetation is characteristic of the Subandean District. In contrast to the SGBR study areas, wet meadows are common within the matrix of upland vegetation at the PAT study areas, especially on the humid end of the precipitation gradient. Botanical nomenclature for PAT follows Correa (1969-1999-).

Fieldwork in the SGBR was carried out in the 2000 (semiarid study area), 2001 (all study areas), and 2002 (the arid study area) growing seasons, and the 1999-2000 (arid study area) and 2000-2001 (all study areas) growing seasons in PAT. In SGBR, 2000 and 2001 precipitation was 80% of normal, and 2002 precipitation was 90% of normal. In PAT, precipitation in 1999-2000 was approximately normal, and in 2000-2001 precipitation was above normal but springtime temperatures were below normal.

Grazing management

While the initial development of the livestock industry in each region, beginning in the mid 19th century in SGBR (Miller et al. 1994) and the early 20th century in PAT (Soriano 1983), featured similar grazing management, or lack of it, 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. Livestock were rarely grazed year-round in SGBR, but instead 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. Presently, although annual spring and summer grazing still occurs, most operations avoid grazing the same pasture in consecutive springs, instead switching from spring to fall use, or resting a pasture entirely, in alternate years. On many public lands in the Columbia Basin of Washington, ecological concerns have led to cessation of grazing within the last twenty years, further reducing the pool of potential study areas. In PAT, year-round grazing is the norm, the exception being some large ranches in the Subandean District that contain both valleys and tablelands, and rotate between winter and summer pastures. Stocking rates in both regions have decreased over time, both for ecological reasons and due to reductions in forage production (Miller et al. 1994, Paruelo and Sala 1992a, Anchorena and Cingolani 1999).

The study areas that I selected reflect these regional differences in grazing management (Table 4.2). First, all three SGBR study areas are grazed exclusively by cattle, and all three PAT study areas are grazed by sheep. In addition to considering evidence in the literature that sheep and cattle have similar effects on SGBR vegetation, I tested this assumption by sampling key response variables at sites within a sheep pasture located close to the semiarid SGBR study area, directly east of Ellensburg, WA. Second, while grazing is seasonal at the SGBR study areas, it is year-round at the PAT sites. Management varies further among the three SGBR study areas: the arid location is grazed from March through May in alternate years, the semiarid location is grazed annually spring through fall, and at the subhumid location, grazing changes from spring/early summer to late summer/fall in alternate years. Unlike the SGBR arid and semiarid study areas, which were originally grazed quite intensively (D. Peterson, BLM, pers. comm.), grazing at the subhumid location was rotated from its inception (B. Billingsley, Washington DNR, pers. comm.). Stocking rates, expressed in terms of expected consumption per m^2, increase with precipitation in both regions, but are generally higher at the PAT study areas, presumably because of the presence of productive wet meadows. For the PAT study areas, I converted stocking rate to expected consumption based on the number of sheep-days grazed in each pasture and an assumed intake of 1 kg dry matter per animal per day. For the SGBR pastures, I used the number of animal unit months (AUM's) per pasture and an intake of 360 kg per AUM (Table 4.2). I consider the implications of these regional management differences in the Discussion.

Grazing intensity gradients and site selection

Water availability is a major influence on livestock distribution in rangelands (Coughenour 1991, Bailey et al. 1996). Livestock density decreases as distance from water increases (Valentine 1947, Lange 1969, Andrew 1988). Many authors have taken advantage of the resulting grazing intensity gradients to study the effects of grazing on vegetation and soils (Andrew 1988, Huntley 1991, Pickup et al. 1998, Turner 1998, Ludwig et al. 1999, Nash et al. 1999, Thrash 2000). I adopted this approach for my research.

Within each of the six study areas, I identified three independent water sources, either streams, springs, or wells. Each water source was located in a different pasture, although in three cases, two water sources were located in the same pasture. I only used pastures in which the stocking rate and the location of water and fences had remained relatively constant over the last twenty years. I then selected 5 to 7 study sites at varying distances from each water source. On each of these transects, I attempted to hold aspect and soil type constant, and only selected sites characteristic of typical native upland communities (I avoided heavily invaded sites). This stratification meant that I could not use fixed distances from water. Sites were never located within the trampled, denuded areas immediately surrounding water. Wherever possible, I also included long-term (> 20 years) ungrazed sites, such as grazing exclosures or fenced roadsides, that were located near each transect. These were available at the SGBR arid and semiarid study areas, and the PAT arid study area.

At 3 to 4 sites on each distance from water transect I built temporary 10x10 m exclosures in order to measure primary production and consumption. I 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.

For all analyses that included the long-term exclosure sites, I transformed the continuous distance from water variable into a categorical variable with three distance classes and a fourth class for the long-term exclosures. Within each study area, I defined the distance classes (Table 4.3) so as to include a roughly equal number of sites in each.

Primary production and consumption

I 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). At each site, I laid out three transects with five sampling stations distributed systematically on each transect. All three transects fit within the 10x10 m temporary exclosures. I used different procedures to estimate production of annuals and perennial forbs, perennial grasses, and shrubs. For annuals and perennial forbs, I used a standard quadrat harvest technique. A 0.5x0.5 m square quadrat was placed over each sampling station on each transect and all aboveground current year's growth of annuals and perennial forbs harvested. The five samples on each transect were pooled, yielding 3 replicates representing an area of 1.25 m^2 each (only four sampling stations per transect were harvested at the subhumid study areas in each region). Biomass samples were dried for 48 hrs at 55°C and then weighed.

To measure the production of perennial grasses, I used a two-step procedure intended to solve problems created by spatial heterogeneity. First, I measured the basal cover of all perennial grass species using 3 40 m line transects laid out in parallel on two sides of each 10x10 m temporary exclosure. Second, I harvested individual plants of all common perennial grass species (generally 2 to 5 species per site) within the temporary ungrazed exclosure as follows: I harvested the two individuals of each species located nearest to each sampling station, recording the longest basal diameter and a second, perpendicular diameter of each plant in order to calculate basal cover using the formula for an ellipse. The ten plants on each harvesting transect were pooled, yielding 3 replicates representing 30 plants total. In the laboratory, these samples were weighed, subsampled by 20%, sorted into live, recently senesced, and dead components, and then the sorted samples were dried and weighed. The proportion live plus recently senesced was used to estimate current year's production for the original, dry-weight corrected sample (Lauenroth et al. 1986). Using the basal cover data from the harvested plants, I calculated the production per unit basal cover of each species. I then used the basal cover data from the 40 m line transects to scale production per unit basal area to production per m^2 for each species. The main assumption of this method is that the form and vigor of plants on the longer 40 m transects is identical to plants located within the 10x10 m exclosure. This assumption should be valid given my effort to select sites that were homogeneous at this scale.

I estimated shrub production using the method of Fernández et al. (1991). This method is based on a relationship between the aboveground production of a particular species, $ANPP_{shrub}$, and two predictor variables: 1) the surface area of the shrub assuming a perfect hemispheric shape, SA, which is calculated from height and diameter measurements, and 2) the production of leaves and twigs within a small quadrat centered on the top of the shrub, which I will label production per plant area, PPA. Then, $ANPP_{shrub} = k^* SA * PPA$ where k is the regression coefficient, estimated by complete harvest of a number of individual shrubs. In order to estimate total production per m^2 of this species, $ANPP_{tot}$, I used belt transects to measure mean shrub surface area, $\overline{SA}$, and shrub density, D. In addition, I harvested small quadrats at the center of a number of randomly selected shrubs to determine mean production per plant area, $\overline{PPA}$. Then, $ANPP_{tot} = k^* D^* \overline{SA} * \overline{PPA}$, where k is the same regression coefficient determined above.

For the arid PAT site, I used regression coefficients for the three dominant shrub species estimated by Fernández et al. (1991). I estimated both D and $\overline{SA}$ using 3 40x2 m belt transects at each site, and $\overline{PPA}$ was estimated by harvesting 25x10 cm quadrats on 5 shrubs of each species (if present) within the temporary exclosures. At the semiarid and subhumid study areas, where the growth form of the dominant shrub *M. spinossum* appeared to differ from the arid study area, I recalibrated the relationship by harvesting 25 randomly selected shrubs, though I required 5 of these to be larger than 1 m in diameter. Due to the higher shrub density at these sites, D and $\overline{SA}$ were calculated using 3 40x1 m belt transects. In the arid and semiarid SGBR study areas, I calibrated the relationship for the dominant shrub *A. tridentata*, harvesting 30 individual shrubs, 5 of which I required to be at least 1 m in height. For subdominant shrub species at the SGBR study areas, I calibrated a relationship based only on shrub density and mean surface area: $ANPP_{tot} = k^{*} D^{*}\overline{SA}$. At all SGBR sites, I used 3 40x1 m belt transects to calculate D and $\overline{SA}$ at each site, and 25x25 cm quadrats to determine $\overline{PPA}$. I tested each relationship using different methods of calculating SA (such as averaging the diameters and height measurements, or using only the diameter mean) and chose the one that minimized least square errors. All analyses used oven-dried weights. Note that production contributed by rare shrub species went unrecorded, but based on the data from the subdominant species I measured, this error was less than 1-2 g m^{-2}.

To measure consumption at grazed sites with temporary ungrazed exclosures, I followed the same protocol in a grazed area immediately adjacent to the exclosure. However, in the paired grazed sample, I only estimated forage production. At all SGBR study areas and the subhumid PAT study area, I defined forage species as all annuals, perennial forbs, and perennial grasses. In the arid and semiarid PAT study areas, unpalatable *Stipa* species contribute a large portion of annual production. After failing to detect consumption of the *Stipa* species at sites located near water, I defined these as non-forage species and did not harvest them in grazed areas. Consumption, therefore, is defined as the forage production in the temporary ungrazed exclosure minus forage production in the adjacent grazed area. Grazing intensity, or utilization, is consumption divided by forage production in the ungrazed area.

The clipping method I used is susceptible to errors introduced by spatial heterogeneity and changes in growth rate following defoliation (Oesterheld and McNaughton 2000). The two-step method I used to estimate perennial grass production, the major forage component, helped minimize errors arising from spatial heterogeneity. I decided that moving the temporary exclosures during the growing season to minimize errors associated by changes in growth rate was not warranted because of the short growing season and low production in these systems.

Indirect measures of grazing intensity

In addition to direct measures of consumption and grazing intensity that I carried out at grazed sites with temporary exclosures, I also used two indirect estimates of grazing intensity at all sites. First, I counted fecal pellets or pats. In PAT, I counted fecal pellets by animal species on 2 40x0.2 m belt transects at each site, following Fernández (1986). In SGBR, I used 2 40x1 m belt transects, the extra width necessary because cattle fecal pats are less dispersed than sheep pellets. Second, I used a semi-quantitative measure of both the frequency and intensity of defoliation (Paruelo and Sala 1992b). This index scores individual plants on the following scale: 0 = no tillers defoliated, 1 = 1 tiller defoliated, 2 = more than 1 but not all tillers defoliated, and 3 = all tillers defoliated. I selected 2 – 3 dominant grass species at each study area, and then averaged the scores of 10 randomly selected individuals of each of these species at each site within the study area. In addition, I measured the basal diameter, leaf height, and inflorescence height of each plant.

Species composition

I distributed 8 1x1 m quadrats systematically on the same 3 40 m transects used to sample perennial grass basal cover and shrub density at each site. I identified all plant species within each quadrat, and visually estimated canopy cover (%) by species. I counted the number of individual plants of each species to determine density. At the arid PAT study area, I estimated density of all species in the 1x1 m quadrat. In all other study areas, I estimated density of perennial grasses and shrubs in the 1x1 m quadrats, but used nested 0.5x0.5 m quadrats to estimate density of annual and forb species.

Soils

To measure soil texture and bulk density, at all sites I extracted 5 soil cores of 5 cm depth from randomly selected bare ground microsites. To measure total soil C and N, I also took soil cores from beneath 5 randomly selected perennial grasses and shrubs. I sampled all three microsites only at the subset of sites also sampled for production. The depth of cores beneath grasses and shrubs was variable to accommodate the accumulation of material around the plant (Burke et al. 1998). To measure the height of these plant "mounds" I used a carpenter's level to run a string horizontally from the center of the plant to the nearest patch of bare ground, and recorded the height of the string above the ground. Total core depth thus equaled 5 cm (the mineral soil component) plus the height of the plant mound. Mound heights were easily measured in PAT, where ground was level and bare soil easily identified, but much harder to measure in SGBR, where the siltier soils preserved greater microtopography and slopes were steeper. Whenever mound height could not be measured with confidence, I cored to 5 cm. Soil cores were immediately air-dried.

Once in the laboratory, I used a 2 mm sieve to separate gravel from soil. Each of these components was then weighed. I determined both total and gravel-free bulk density by averaging the soil weight divided by the core volume of the 5 bare ground samples from each site. 10 g subsamples of all soil samples were oven dried for 24 hours at 100°C to determine moisture content. I aggregated the 5 samples from each microsite (bare, grass, shrub) by combining 25% subsamples of each replicate's moisture corrected dry weight. The aggregated bare ground samples were then used to determine soil texture by the hydrometer method (Gee and Bauder 1986). After grinding subsamples of the aggregated samples in a roller mill, I determined total C and N concentration by combustion using a LECO CHN-1000 analyzer (St. Joseph, MI).

Scaling the C and N concentration data up to total C and N (g m^{-2}) required first multiplying total C and N concentrations by the combined moisture-corrected soil weight of all 5 microsite samples at each site. This product, the total C and N per core, was divided by the surface area of the core (in m^2) and then multiplied by the proportion of ground covered by the corresponding microsite, determined by the canopy cover estimates (bare ground = 1 – grass – shrub). Total C and N (g m^{-2}) is the sum of the bare, grass, and shrub fractions.

Statistical analysis

Calculating the uncertainty of the production estimates is difficult because so many estimated parameters are added and multiplied. Therefore, I estimated uncertainty for individual sites using a Monte Carlo simulation approach (Lauenroth 2000). Based on the sampled data, I calculated the mean and variance of the following parameters: annual and forb production (g m^{-2}), grass basal cover (m/m), grass production per plant area (g m^{-2}), shrub density (m^{-2}), shrub production per plant surface area (g m^{-2}), and shrub surface area (m^2). These means and variances were used to generate a lognormal distribution for each parameter. A value was drawn at random from each of these distributions, and then these values were added and multiplied as necessary to produce an estimate of total production (g m^{-2}). I repeated this process 10,000 times. The variance of these 10,000 simulations is an estimate of the uncertainty in my field-based estimate of production for the given site.

To analyze the effect of distance from water, a proxy for grazing intensity, on production, composition, and soil response variables, I used linear mixed models. For each response variable, I started the analysis with three fixed factors and their interactions: 1) region—PAT and SGBR, 2) precipitation—arid, semiarid, subhumid, and 3) distance from water class. I included transect, nested within region by precipitation, as the random factor. I also included annual potential radiation, which integrates slope and aspect (Swift, Jr. 1976), as a covariable. For soil response variables, I included soil sand fraction as a covariable as well. I removed interactions and independent variables (when not included in significant interactions) not significant at $\alpha = 0.10$. Because of the relatively limited number of independent variables, I could check all plausible combinations, and did not have to rely on automated variable selection. For production and composition variables, I included distance class in the model even when it was not statistically significant, because grazing effects were of primary interest. I tested for significant differences among least squares means setting $\alpha = 0.05$. 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 results were averaged by region or precipitation, least squares means for distance class 4 are poorly estimated. I checked all residuals for normality and transformed response variables as necessary (Appendix 4.1). In these cases, reported least squares means were back-transformed, which may result in a slight underestimate in the case of log transformations, but preserves ratios among the means. All analyses were run in SAS 8.2 using Proc Mixed (SAS Institute, 1999). I selected the Satterthwaite option to estimate degrees of freedom and used type III sum of squares due to the unbalanced design.

Models of production responses used 2001 growing season data from SGBR and 2000-2001 for PAT. For each site where 2 years of production data were available (SGBR arid and semiarid, PAT arid), I also constructed a mixed model with distance class and year as fixed effects, and transect as a random effect. I used these repeated measures tests to confirm the results from the single year models that included all study areas.

To analyze the effect of grazing and environmental variables on species composition at each study area, I used constrained ordination, analogous to a multivariate multiple regression. I chose Redundancy Analysis (RDA) over Canonical Correspondence Analysis, an alternative constrained ordination method, after determining that changes in the abundance of most species along the grazing intensity gradients were linear and not unimodal. RDA explains as much variation as possible in a matrix of response variables using linear combinations of explanatory variables. It is also possible to introduce covariables, in which case the explanatory variables explain the variation that remains after applying the covariables. I used square-root transformed canopy cover estimates of all species occurring in at least 3 sites as the response variables. The covariables 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. Thus, for each of the six study areas, I used RDA to calculate the percent of variation in species composition explained by grazing variables after accounting for environmental variation. Because the abundance of all species was measured in the same units, RDA was based on the covariance, not the correlation, matrix. For graphical display, I focused scaling on intersite differences. I ran these analyses in Canoco 4.0 (ter Braak and Smilauer 1999).

RESULTS

Calibration of production methods

My recalibration of the relationship $ANPP_{shrub} = k^* \; SA * PPA$ for *M. spinossum* at the PAT semiarid and subhumid study areas produced almost the same value of *k* (0.377 instead of 0.37) found by Fernández et al. (1991) for *M. spinossum* at the arid PAT site. The calculation of surface area (*SA*) was based only on shrub diameters, ignoring height. This relationship explained 93.5% of variation about the origin in individual shrub biomass ($n = 25$).

The calibration of this relationship for *A. tridentata* at the SBGR study areas also produced a good fit (Table 4.4, Fig. 4.2), with an r^2 of 0.898. Relationships based only on shrub size for *A. tripartita* and *Chrysothamnus viscidiflorus* explained over 90% of variation, while the relationship for the smaller shrub *Eriogonum microthecum* explained 84% of variation (Table 4.4, Fig. 4.2).

Total production at 12 sites in the arid PAT study area harvested in January 2001 ranged from 43 to 85 $g/m^2/yr$ with a mean of 59. Across these twelve sites, grasses contributed on average 35 $g\ m^{-2}$ and shrubs 21 $g\ m^{-2}$. In January 2000, I estimated a mean of 86 $g/m^2/yr$ across the 12 sites, with most of the increase coming from the grasses.

Monte Carlo simulations estimated values of total production within 0.1 to 5.8% of the observed values, with an average absolute difference between simulated and observed of 2.3%. Coefficients of variation (CV) ranged from 7 to 27% with a mean of 19%.

Consumption and grazing intensity

Forage consumption, measured by direct harvest, tended to be higher at SGBR compared to PAT study areas, despite the fact that stocking rates were higher at the PAT sites (Fig. 4.3). In fact, all consumption measurements in PAT fell below expected consumption based on stocking rates, whereas at all SGBR study areas, consumption at many sites exceeded the expected pasture-wide mean. No strong trends emerged across the distance from water transects, though the lowest consumption values tended to occur at locations farthest from water at all study areas except subhumid PAT (Fig. 4.3).

Grazing intensity, the proportion of forage production consumed, likewise was higher in SGBR than PAT, especially in the semiarid and subhumid study areas (forage was more narrowly defined at the arid PAT study area) (Fig. 4.4). Across the distance from water transect, grazing intensity generally declined, though in some study areas the sites with the highest grazing intensity occurred at intermediate distances from water.

The indirect measures of grazing intensity, taken at all sites in each study area, supported these trends. Average defoliation index declined with increasing distance from water, but, as with the direct measure of grazing intensity, at some study areas the highest values of the defoliation index occurred at intermediate distances (Fig. 4.5). Fecal counts also declined with increasing distance from water, but many of the highest values occurred closest to water rather than at intermediate distances (Fig. 4.6).

Grazing effects on functional group abundance

For perennial grass basal cover, the region by precipitation by distance interaction was significant (Fig. 4.7, Appendix 4.1). Basal cover increased dramatically 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. Basal cover was higher on average at PAT sites, but precipitation had no significant effect. At the SBGR arid and semiarid study areas, basal cover of the dominant bunchgrass *A. spicatum* was zero at some sites closest to water. Basal cover of the dominant PAT bunchgrasses was always greater than zero.

Perennial grass 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. 4.8, Appendix 4.1). Region did not have an effect, 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 perennial grass production (Appendix 4.2). When this test was run on palatable perennial grasses only, excluding the *Stipa* species, production increased significantly, ranging from a least squares mean of 5.3 g m^{-2} in sites closest to water to 23.8 g m^{-2} in long-term ungrazed sites (Appendix 4.2).

Shrub canopy cover, in contrast, decreased significantly with distance from water in both regions (Fig. 4.9A, Appendix 4.1). The region by precipitation interaction was significant because shrub cover was relatively constant across the precipitation gradient in PAT, but fell sharply in the SGBR subhumid study area (Fig. 4.9B). Results for shrub production paint a slightly different picture. Using one year of data, distance had no effect, but the region by precipitation interaction was again significant (Appendix 4.1). The repeated measures tests, however, showed that shrub production was significantly higher at locations close to water in the arid and semiarid SGBR study areas, but distance had no significant effect at the arid PAT study area (Fig. 4.10, Appendix 4.2).

The density of annual plants increased with precipitation and decreased with distance from water, especially in SGBR and at higher levels of precipitation (Appendix 4.1). The production of forbs plus annuals varied significantly with distance only at the arid PAT site, where the highest values occurred in long-term ungrazed sites (Fig. 4.11, Appendix 4.1). Forb and annual production was much lower in this study area than any other.

Total production increased with distance from water in SGBR but not PAT (Fig. 4.12, Appendix 4.1). Total production increased across precipitation gradients in both regions, though most of the difference occurred between the semiarid and subhumid study areas in SGBR, while in PAT the difference occurred between the arid and semiarid study areas. Repeated measures tests confirmed the distance result: 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 4.2).

Species richness and composition

Grazing had either weak or no effects on species richness, depending on spatial scale. The number of species per 1 m^2, which was the average species richness across the 24 quadrats at each site, was not significantly influenced by distance from water at $\alpha = 0.05$, but was significant at $\alpha = 0.10$, with peaks in species richness at intermediate distances (Fig. 4.13A, Appendix 4.1). Richness at this scale increased with precipitation equally in both regions (Fig. 4.13B). 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, with greater increases in species richness across the precipitation gradient in SGBR than in PAT (Fig. 4.14, Appendix 4.1).

Averaging across region, the number of non-native species per site was significantly higher close to water than in more distant grazed sites, but was not higher compared to long-term ungrazed sites (Fig. 4.15A, Appendix 4.1). More strikingly, while 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. 4.15B). While the PAT data are dependable, the SGBR must be viewed cautiously because I made an effort to avoid heavily invaded sites in that region.

Distance from water had no effect on the number of annual species per site, but the region by precipitation interaction was significant. The number of annual species was similar at the arid SGBR and PAT study areas, with 4.7 and 3.4 annuals on average. Differences between the SGBR and PAT semiarid (11.0 vs. 3.2) and subhumid (13.1 vs. 6.5) study areas were significant (Appendix 4.1).

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 4.5). Variation explained at the semiarid and subhumid study areas was similar in both regions (59 to 64%). At the arid SGBR site, abundance of *A. tridentata* and *Poa secunda* was correlated with greater defoliation and decreased with distance to water, while *A. spicatum* and the palatable *Poa cusickii* increased with distance from water and in long-term ungrazed sites (Fig. 4.16A). Trends at the semiarid SBGR study areas were similar, though bare ground and *Sitanion hystrix* were more strongly associated with heavily grazed sites than *P. secunda* (Fig. 4.16B). At the subhumid SGBR study area, high abundance of *Stipa comata* and bare ground was associated with sites close to water, whereas *F. idahoensis* and *A. spicatum* were more abundant in sites far from water (Fig. 4.16C). Grazing increasers in arid PAT included *Carex andina*, *S. speciosa*, *M. spinossum*, and the rhizomatous *Poa lanigunosa*, while *Bromus pictus* and *P. ligularis* were associated with long-term ungrazed sites (Fig. 4.16D). 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, transect appeared to explain much of the variation in species composition, separating species common to the Occidental District, such as the *Stipa* spp., from species characteristic of the Subandean district, such as *F. pallescens* and *F. magellanica* (Fig. 4.16E). *F. pallescens* was a strong grazing decreaser at the subhumid PAT study area, while *F. magellanica* and *M. spinossum* increased with grazing pressure (Fig. 4.16F).

Effects of sheep grazing on sagebrush steppe

In the one sheep pasture that I sampled, trends in functional type abundance with distance from water were similar to the results from 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 (Fig. 4.17A-C). 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 (Fig. 4.17D).

Soils

Distance from water had no significant effect on total soil C or N (Appendix 4.1). Concentrations of C and N were lowest in bare ground microsites at all study areas and highest under shrubs at the most arid sites, but grass and shrub soils had similar C and N concentrations at the semiarid and arid sites (Fig. 4.18). Observed values of total soil organic matter increased with precipitation in both regions, but soil N values at the arid and semiarid sites were higher in SGBR than PAT (Fig. 4.19). When soil sand fraction was included in the statistical model, however, this region by precipitation interaction remained significant, but the regional difference reversed: soil C estimated by this model was higher in PAT than SGBR (Fig. 4.20, Appendix 4.1). Results for soil N were qualitatively identical.

Bulk density increased with increasing sand content and decreased with increasing precipitation, though this decrease was more dramatic in Patagonian than sagebrush steppe (Appendix 4.1). Distance from water had a weak ($p = 0.091$) effect on bulk density at the arid sites, where exclosures had the lowest bulk density, and at the subhumid sites, where sites at intermediate distances from water had the lowest bulk density.

DISCUSSION

Although many production and composition responses to grazing were consistent with a longer evolutionary history in Patagonia, my measurements of consumption and grazing intensity suggest important differences in grazing pressure in sagebrush and Patagonian steppe. Therefore, rather than try to compare the relative response of these two ecosystems per unit grazing pressure, this discussion focuses on comparing the degree of change in ecosystem structure and function caused by decades of livestock grazing typical of each region. I begin by evaluating my field methods. Next, I describe the causes of differences in consumption and utilization, and then propose that these contrasts in grazing pressure determined the differences in the response of vegetation. Finally, I consider alternative explanations for the contrasting grazing responses of these ecosystems, weighing the importance of the evolutionary history of grazing against abiotic differences.

Evaluation of production estimates

I evaluated the quality of my total production estimates in two ways. First, I compared my estimates from the arid PAT study area to estimates made using traditional methods at a nearby site, and second, I analyzed the uncertainty of the estimates. Jobbágy and Sala (2000), using 10 years of data, found that total production ranged from 21 to 75 g m^{-2}, with a mean of 56 g m^{-2}. Production was evenly split between grasses and shrubs. My estimate of total production, based on a wider range of sites, was 59 g m^{-2} in 2001 and 86 g m^{-2} in 2000. Across these twelve sites, grasses contributed on average 35 g m^{-2} and shrubs 21 g m^{-2}, but shrub production was higher in some individual sites. My estimates for grasses are higher than those of Jobbágy and Sala because I included recently senesced material as current year's production. This increased my estimate of the total by 7 g m^{-2} in 2001 and 27 g m^{-2} in 2000. Removing this difference, my estimates of production fall comfortably within the historic range. Comparisons of my estimates to those made in the same years using traditional methods are more difficult to evaluate. In 2001, the traditional methods produced an estimate of 78 g m^{-2}, within the range of estimates I made in the same year, but well above the mean of 59 g m^{-2}. The difference is greater if I remove the senescent component from my estimates. The traditional estimate of 51 g m^{-2} made in 2000 is fairly close to my mean from that year if the senescent component is removed. However, the fact that shrubs contributed well over 50% of production in both years at the site where traditional sampling was used suggests differences in composition compared to my sites, where shrub production was lower (Sala unpublished data).

The Monte Carlo simulations provided an estimate of intra-annual variability in production estimates caused by measurement error and spatial variability. My harvesting method produced a mean coefficient of variation of 19% for all vegetation, compared to a mean CV of 31% just for grass production harvested using traditional methods (nine years of data from Jobbágy and Sala 2000). My method of estimating grass production, designed to reduce variability created by spatial heterogeneity, successfully reduced uncertainty compared to traditional quadrat methods.

Grazing intensity and consumption

The grazing intensity data confirmed that distance from water gradients do represent gradients in grazing pressure. Utilization, the defoliation index, and fecal counts all tended to decrease as distance from water increased. But the great variability in these data, and the fact that the highest values of utilization and defoliation frequently occurred not at sites closest to water but at intermediate distances, underscores the difficulty of measuring grazing intensity. This variability makes more sense if we view distance from water as a proxy for historical, not current, grazing intensity. When livestock were first introduced to these pastures, it is reasonable to assume that vegetation was relatively homogeneous and utilization decreased steeply with distance from water. As forage availability near water declined over time (Pickup et al. 1998), consumption near water would have declined as well. More surprising is that, as suggested by my data, the proportion of available forage consumed also should decline, indicating that livestock began choosing to forage in areas farther from water. Simulations of livestock foraging along distance from water gradients indicate that such a pattern can develop under a wide range of foraging rules (Appendix I). Therefore, historical effects of grazing may result in current low grazing intensity in degraded sites very close to water, and high grazing intensity at sites farther from water that offer more abundant forage.

Despite the higher stocking rates in PAT, absolute consumption was lower than in SGBR. One possible explanation for this paradox is errors in my measurements. At the arid PAT study area, I introduced an error by ignoring consumption of the dominant but unpalatable *Stipa* species. These grasses provide winter forage to sheep (Somlo et al. 1992), but because consumption was lower than the variability in my biomass estimates for these species, I could not quantify it. Although unmeasured consumption of *Stipa* could explain the differences between expected and observed consumption at the arid PAT study area, this error is unlikely to be large enough to explain the difference between observed consumption at the arid PAT and SGBR study areas. More importantly, it cannot explain low levels of consumption in semiarid and subhumid PAT, where I successfully quantified consumption for all herbaceous species. A second type of error would be introduced if PAT plants compensated more following defoliation than SGBR plants. By increasing growth rates following defoliation, the ungrazed-grazed biomass difference and my resulting consumption measurements would decrease. The results from the defoliation index allow me to reject this explanation: PAT grasses were not defoliated as frequently or intensely as SGBR grasses, especially in sites near water.

If measurement errors do not explain the lower consumption in PAT, then a real ecological difference must exist. One potentially important difference is the presence of wet meadows in the PAT pastures, especially at the semiarid and subhumid sites. These highly productive sites, while only a small portion of the total landscape, provide a very large component of sheep forage (Somlo et al. 1992). The upland vegetation is used most intensively in winter, when the wet meadows are frozen and the vegetation dormant. 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 I studied, explaining why observed consumption was so much higher than expected.

The importance of wet meadows in PAT, however, does not explain why upland forage is not better utilized. Utilization in semiarid and subhumid PAT was much lower than in SGBR, and would be lower in arid PAT as well if I included *Stipa* species as forage. 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 in fact stocked to economic capacity (Soriano and Paruelo 1990, Paruelo and Sala 1992a, Golluscio et al. 1998). Currently, lambing rates at the semiarid and arid study areas decrease in response to small increases in stocking rate (Anchorena and Cingolani 1999, Borelli 2001).

A better explanation for the low consumption and utilization in upland PAT vegetation is the poor forage quality of the dominant grasses. Nitrogen concentrations of the dominants *S. speciosa* and *S. humilis* in arid PAT were 0.72 and 0.77% for mature green leaves, and C:N ratios were about 60:1 (Chapter 3). *P. ligularis*, the preferred forage species, was no better, with a N concentration of 0.73% and a similar C:N ratio, but a higher concentration of cell solubles. Forage quality at the subhumid PAT study area is higher. *F. pallescens* and *P. ligularis* had N concentrations in green leaves of 1.0 and 0.9% and C:N ratios of 44:1 and 48:1, respectively. In arid and semiarid SGBR, by contrast, N concentrations in green leaves of the dominant plants ranged from just over 1.0 for *A. spicatum* to 1.5 in *P. secunda*, and C:N ratios for these species were 41:1 and 28:1. Forage quality was also higher at the subhumid SGBR study area, where N concentrations for *F. idahoensis* and *A. spicatum* were 1.1 and 1.5%, and C:N ratios 37:1 and 30:1 (Chapter 3). Other data on N content in all aboveground tissue of PAT grasses (Borelli 2001) and of SGBR species (Murray et al. 1978, Ganskopp and Bohnert 2001) are consistent with my results. These differences in forage quality can have large consequences in animal performance. As forage quality decreases, the rate of passage through a ruminant's gut slows. Given extremely poor forage, the rate of passage slows enough to limit intake—the animal simply lacks space in its gut for more food. Ruminants suffer bulk limitation and decreased intake when forage crude protein content falls below 7-10% (Allison 1985), equivalent to N concentrations of 1.12 – 1.6%, close to the values for SGBR forage species, but below the values for the PAT plants. Field evidence supports the hypothesis that sheep in semiarid Patagonian sites may be nutrient limited in digestion and intake (Borelli 2001). Golluscio et al (1998) reported that urea supplementation led to a significant increase in animal weight gain and in the frequency and intensity of defoliation of unpalatable *Stipa* species.

Trends in species diversity

The absence of grazing effects on species diversity that I observed is inconsistent with the predictions of many studies (Milchunas et al. 1988, Belsky 1992, Olff and Ritchie 1998, Collins et al. 1998). The Milchunas 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 higher precipitation sites. The Olff and Ritchie model predicts decreases in diversity at dry, fertile sites, such as sagebrush and Patagonian steppe. The responses I 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. These results are more consistent with Stohlgren et al. (1999), who found that grazing in Rocky Mountain grasslands increased richness at the 1 m^2 scale, but had no effect at the 1000 m^2 scale. Diversity appears to be influenced by a grazing-spatial scale interaction that current models do not include.

Precipitation, not grazing intensity, was the primary determinant of plant diversity. The observed increases in diversity with increasing precipitation are consistent with data from other grasslands (Gross et al. 2000). That richness increases more rapidly along the SGBR precipitation gradient may be a result of differences in area: the small landmass of temperate South America probably limits the regional species pool.

Although I did not design this study to assess invasibility, some of the data on non-native species numbers deserve attention. The number of non-native species increased dramatically along the PAT precipitation gradients, rising from a mean of zero at the arid study area to more than 3.5 exotics 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 non-natives with distance from water in both regions suggest that grazing can facilitate invasion in these systems. The relatively high number of non-natives in long-term ungrazed sites is likely a spurious result caused by the proximity to roads of many of these sites.

Effects of grazing on primary production and species composition

Comparing SGBR study areas to the PAT arid study area, differences in the effects of grazing on production and species composition were large and consistent with a longer evolutionary history of grazing in PAT. Both perennial grass abundance, measured as cover or production, and total production increased with distance from water in SGBR, but were unaffected by grazing at the arid PAT study area. Shrub abundance, on the other hand, decreased with distance from water in SGBR, but, again, was not affected in arid PAT, at least when considering 2 years of production data. Finally, the constrained ordinations based on grazing variables explained a much higher percent of variation in species composition in SGBR (59 – 74%) than in arid PAT (43%). The only response variable for which arid PAT showed more sensitivity to grazing than SGBR was production of forbs and annuals. For all other response variables, arid PAT was much less sensitive to grazing effects than SGBR, consistent with a hypothesis of greater adaptation to grazing in the Patagonia flora.

Comparing SGBR to the subhumid PAT study area, I found fewer differences in the effects of grazing, but they were again consistent with a longer evolutionary history of grazing in PAT. Perennial grass abundance increased with distance from water in subhumid PAT, similar to SGBR but quite distinct from the lack of response in arid PAT. Percent of variation in species composition explained by grazing (60%) was also similar to SGBR. Total production, however, was not significantly affected by grazing anywhere in PAT, but increased with distance from water at all SGBR study area. Also, while the dominant SGBR bunchgrass, *A. spicatum*, was locally extirpated in a number of sites closest to water, the dominant bunchgrass in subhumid PAT, *F. pallescens*, while suffering decreases in abundance, was present even at the sites closest to water. At the semiarid PAT study area, responses for some variables were similar to arid PAT, while responses for other variables were similar to subhumid PAT. These results are expected under the Milchunas et al. (1988) model, which predicts that differences in the grazing response of ecosystems with long vs. short evolutionary histories of grazing will decrease as precipiation increases.

The contrasting effects of grazing in SGBR and PAT are not simply a result of differences in grazing management. One management difference that could confound the comparison is the use of cattle in SGBR and sheep in PAT. However, both the literature and my limited sampling in one sheep pasture demonstrated that spring grazing by cattle and sheep have similar effects on sagebrush steppe vegetation. Both animals preferentially graze perennial grasses, leading to a decline in grass abundance and, often, an increase in shrub abundance. Although sheep are more selective, showing a greater preference for forbs (Grant et al. 1985), defoliation of perennial grasses in the sheep pasture (index values of 1.6 and 1.7 in the sites nearest water) was similar to defoliation in the cattle pastures. It is unlikely that my results would be different if I had studied SGBR grazed by sheep. Sheep and cattle in PAT also have similar diets (Somlo et al. 1992).

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 difference in grazing effects? After all, holding stocking rates constant, spring grazing will concentrate the impacts of defoliation during the growing season, when plants are most sensitive. But history and theory suggest that continuous grazing in SGBR would lead to more severe vegetation change, increasing, rather than decreasing, differences with PAT. Practical experience dictating that periods of rest during the flowering period are necessary to prevent loss of the dominant SGBR bunchgrasses is supported by experimental results (Daubenmire 1940, Blaisdell 1949, Caldwell et al. 1981, Ganskopp 1998). While continuous grazing would reduce growing season consumption on average, it will also lead to a less uniform distribution of livestock (Bailey et al. 1996), increasing negative impacts in sites close to water and reducing impacts far from water. Thus, continuous grazing in SGBR would result in even more dramatic changes in vegetation along distance from water gradients.

I propose that differences in grazing effects in SGBR and PAT are driven by differences in consumption and utilization, which are, in turn, determined by forage quality. Forage quality is lowest in arid PAT, the location least affected by grazing. Forage quality is highest in SGBR, the locations most affected by grazing. Vegetation at the subhumid PAT study area was intermediate in both forage quality and sensitivity to grazing. In arid PAT, the presence of low quality, unpalatable dominant bunchgrasses buffers the system. Utilization is focused on a small group of palatable grasses and forbs, explaining why both forb and palatable grass production decreased with grazing, but total grass and overall production were unaffected. In SGBR, virtually all herbaceous biomass is palatable and relatively nutritious, promoting higher consumption and, as a result, greater impacts on vegetation. The importance of forage quality in driving grazing impacts on vegetation begs the question, what determines the forage quality of dominant species?

The origin of poor quality forage in Patagonia

The low nitrogen and high fiber content of the dominant perennial grasses in Patagonia could have evolved as a defense against guanaco grazing. Such generalized defenses in the grasses would be consistent with other evidence of grazing adaptations in the Patagonian flora such as the presence of spines and thorns on Patagonian shrubs (Lauenroth 1998) and the ability of repeatedly grazed grasses to adopt prostrate growth habits (Chapter 3, M. Aguiar pers. comm.). The higher forage quality of SGBR plants, and their lack of adaptations to grazing, might reflect the relative lack of evolutionary grazing pressure. However, the evolution of differences in forage quality could be driven by differences in abiotic factors as well as grazing history.

The length of the growing season is one factor that could influence forage quality. A satellite-derived vegetation index showed that, on average, growing season tends to be longer in PAT than SGBR (Chapter 2). This result makes sense given the coarser soils of PAT, which allow deeper infiltration of precipitation and reduce evaporative losses, and lower summer temperatures in PAT, further reducing evaporative demand (Chapter 2). The ecological implication is that plants must grow faster in SGBR than in PAT in order to complete their growth cycle before soils dry out. Fast growth is associated with lower leaf lifespan, higher N leaf tissue, and higher specific leaf area (Reich et al. 1992, 1999). Fast-growing leaves also are more palatable and nutritious to herbivores than slower-growing leaves (Grime et al. 1997). Growing season length, and its influence on plant tissue quality, however, does not explain why plant quality should change dramatically along the Patagonian precipitation gradient. Furthermore, it is unclear why plants should not evolve to grow quickly in Patagonia, regardless of the growing season length, if not to resist herbivores.

Nitrogen limitation, caused by extremely coarse soils, may be more likely to cause poor forage quality in the Patagonian grasses. The total soil C and N data support this hypothesis. We should not be surprised that grazing had no significant effect on soil organic matter in either ecosystem, since this variable may require centuries to respond to changes in aboveground vegetation. The higher variability in soil organic matter in SGBR may simply reflect the greater environmental heterogeneity among these sites, which varied greatly in terms of slope and aspect compared to the level PAT sites. The key result from this analysis was the extremely low total soil C and N in arid PAT compared to arid SGBR, but no clear difference between the subhumid study areas. Differences in soil texture explained these results: soils at the arid and semiarid PAT study areas are much coarser than the corresponding SGBR sites, while the difference in texture between the subhumid areas is smaller. In fact, the statistical analysis suggested that, adjusting for sand content, the semiarid and subhumid Patagonian sites accumulate significantly more soil organic matter than the corresponding sagebrush sites. In other grassland systems, coarse soils accumulated less total N and experienced higher N mineralization rates than finer textured soils (Schimel et al. 1985a,b, Aguilar and Heil 1988, Aguilera et al. 1988), which probably stabilized N through adsorption and aggregation onto clays (Schimel et al. 1985a). Such low total soil N--concentrations in bare soil at all arid PAT sites were below 0.05%--implies a strong potential for nitrogen limitation, and would explain the low N content of arid PAT grasses. In subhumid PAT, the loamier soils accumulate more N, ameliorating the N limitation and permitting higher quality forage to grow.

The Milchunas model may be successful precisely because it does not attempt to unravel the mechanics of plant-animal coevolution. It simply assumes that coevolution must have occurred where populations of native grazers were high, and, as a result, plants in those ecosystems will possess adaptations to grazing. This approach successfully predicted that grazing would have greater effects on vegetation in PAT than in SGBR, though the evidence from arid PAT is more consistent with the prediction than evidence from subhumid PAT. I argue that the proximate cause for the regional contrast in grazing impact is the difference in plant traits related to forage quality, which results in lower consumption in PAT compared to SGBR. To identify the ultimate cause of the regional contrast, which requires unraveling the roles of grazing history and pre-existing differences in the abiotic environment, we must move beyond the Milchunas model. This case study suggests that an understanding of abiotic environments may allow predictions about the direction of coevolution. Nitrogen limitation created by coarse soils in PAT probably prevented the evolution of grazing tolerant grasses like those that form grazing lawns (McNaughton 1984) in the shortgrass steppe of North America or the Serengeti. 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 high animal densities will not characterize all grazing adapted ecosystems. Where abiotic conditions are less favorable, as in arid Patagonia, a negative feedback and lower animal densities will be the products of coevolution. Although well-defended plants inevitably limit livestock production, they make the ecosystem more resistant to overgrazing than one dominated by undefended plants such as the sagebrush steppe.

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Table 4.1. Study area information.

	Site name	Latitude	Long.	MAP (mm)	MAT (°C)	Soil texture	Dominant species
Sagebrush steppe	Wanapum State Park	46.95 N	120.01 W	170	11.5	Silt loam, Sandy loam	*A. spicatum,* *A. tridentata*
	Ellensburg	46.86 N	120.42 W	~250	8.6	Silt loam, Loam	*A. spicatum,* *A. tridentata*
	N. Douglas Cty	48.00 N	119.30 W	300+	~7.5	Sandy loam Silt loam	*F. idahoensis,* *A. tripartita*
Patagonian steppe	Río Mayo	45.39 S	70.25 W	154	8.6	Sand	*S. speciosa,* *M. spinossum*
	Lago Blanco	45.93 S	71.37 W	~250	~7.5	Sand	*F. pallescens,* *M. spinossum*
	Valle Huemules	45.97 S	71.53 W	~400	6.5	Loamy sand	*F. pallescens,* *M. spinossum*

Table 4.2. Grazing management at each study area. Expected consumption, based on stocking rates, is shown in $gm^{-2}yr^{-1}$.

	Sagebrush steppe arid	 semiarid	 subhumid
Grazers	cattle	cattle	cattle
Season	spring, alternate years	spring-fall, every year	spring/summer alternating summer/fall
Consumption	5	13.5	18 - 20

	Patagonian steppe arid	 semiarid	 subhumid
Grazers	sheep	sheep	sheep
Season	continuous, every year	continuous, every year	continuous, every year
Consumption	6.5 - 14	26 - 30	26 - 30

Table 4.3. Distance-from-water classes at each study site defined by actual distance (km). "Exclosures" are sites that have not been grazed by livestock for at least 20 years; the number of sites in each study area meeting this criterion is shown in parentheses.

	Sagebrush steppe			Patagonian steppe		
Dist. class	arid	semiarid	subhumid	arid	semiarid	subhumid
1	< 0.5	< 0.4	< 0.5	< 0.5	< 0.5	< 0.5
2	0.5 – 1.0	0.4 – 1.4	0.5 – 1.0	0.5 – 2.0	0.5 – 1.1	0.5 – 1.0
3	> 1.5	> 1.4	> 1.0	> 2.0	> 1.1	> 1.0
Exclosures	(2)	(4)	(0)	(2)	(0)	(0)

Table 4.4. Models used to estimate shrub leaf and fine twig production per m^2 in Sagebrush steppe. Shrub surface area was calculating using the formula for a hemisphere ($2\pi r^2$). "*SAd*" denotes that *r* was based on two shrub diameter measurements, while *r* used in "*SAdh*" was the mean of diameter and height measurements. Density "*D*" is shrubs m^{-2}, and "*G*" is the production per plant unit surface area (g cm^{-2}). All regressions were forced through the origin. "*k*" is the regression coefficient, and "r^2" measures the proportion of variability in observed production about the origin explained by regression.

Species	Model	*k*	r^2	*n*
Artemisia tridentata v. tridentata	$a \times SAdh \times D \times G$	0.2480	0.898	30
Artemisia tripartita	$a \times SAd \times D$	0.0086	0.915	30
Chrysothamnus viscidiflorus	$a \times SAd \times D$	0.0052	0.956	25
Eriogonum microthecum	$a \times SAdh \times D$	0.0027	0.844	25

Table 4.5. Results of redundancy analysis (RDA). Shown is the percent 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 4 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).

Ecosystem	Study area	Variation explained	RDA 1	RDA 2	RDA 3	RDA 4
	arid	74	.180	.055	.045	.018
Sagebrush steppe	semiarid	60	.203	.127	.049	.025
	subhumid	59	.183	.067	.035	.026
	arid	43	.203	.074	.063	.028
Patagonian steppe	semiarid	64	.275	.115	.062	.035
	subhumid	60	.226	.136	.065	.023

Appendix 4.1. F-tables for mixed-model tests. "region" refers to Sagebrush vs. Patagonian steppe, "ppt" refers to arid, intermediate, and semiarid study areas within each region, "distance" is the distance-from-water class, and "radiation" is potential radiation based on slope and aspect.

Dependent variable	Independent variables	Num DF	Den DF	F	*p*
a. Perennial grass basal cover					
	region	1	16.5	7.76	0.013
	ppt	2	12.5	0.80	0.47
	region*ppt	2	12.1	5.86	0.017
	distance	3	74.4	18.29	<0.0001
	region*distance	3	74.2	0.24	0.87
	ppt*distance	5	73	3.28	0.010
	region*ppt*distance	4	72.6	2.37	0.061
b. Perennial grass above-ground production (log transformed)					
	region	1	13	2.45	0.14
	ppt	2	12.1	4.74	0.030
	region*ppt	2	12.2	15.87	<0.001
	distance	3	34.7	10.55	<0.0001
	region*distance	3	34.6	1.91	0.15
	ppt*distance	5	33.3	1.01	0.42
	region*ppt*distance	4	33.1	2.64	0.051
c. Shrub canopy cover (square root transformed)					
	region	1	11.4	7.14	0.021
	ppt	2	11.3	3.93	0.051
	region*ppt	2	11.3	9.51	0.004
	distance	3	85.4	4.86	0.004
d. Shrub aboveground production (log transformed)					
	region	1	52	33.08	<0.0001
	ppt	2	52	1.95	0.15
	region*ppt	2	52	12.27	<0.0001
	distance	3	52	1.33	0.27
e. Density of annual plants (square root transformed)					
	region	1	21.3	0.81	0.38
	ppt	2	14.7	51.82	<0.0001
	distance	3	76.1	17.12	<0.0001
	ppt*distance	5	75.4	3.28	0.010
	region*distclass	3	75.8	3.01	0.035
f. Forb aboveground production (log transformed)					
	region	1	16.1	1.73	0.21
	ppt	2	12.2	8.19	0.006
	region*ppt	2	11.9	11.86	0.002
	distance	3	31.4	2.40	0.087
	region*distance	3	30.5	8.28	<0.001
	ppt*distance	5	30.2	2.16	0.085
	region*ppt*distance	4	30.9	2.95	0.036
	radiation	1	34.1	6.37	0.016
g. Total aboveground production					
	region	1	18.3	0.99	0.33

ppt	2	12.4	12.58	0.001
region*ppt	2	12.4	3.55	0.060
distance	3	42.6	3.17	0.034
region*distance	3	42.1	2.84	0.049
radiation	1	36.8	3.92	0.055
h. Mean species richness per 1-m^2 quadrat				
region	1	13.9	0.00	0.97
ppt	2	13.8	36.17	<0.0001
distance	3	82.7	2.24	0.089
i. Species richness per site (sum across 24 1-m^2 quadrats)				
region	1	12.5	15.70	0.002
ppt	2	12.4	70.80	<0.0001
region*ppt	2	12.4	5.97	0.015
distance	3	85.8	0.67	0.58
j. Non-native species richness per site (sum across 24 1-m^2 quadrats)				
region	1	11.5	10.01	0.009
ppt	2	11.5	25.83	<0.0001
region*ppt	2	11.4	7.20	<0.001
distance	3	83.8	6.83	<0.001
k. Annual species per site (sum across 24 1-m^2 quadrats)				
region	1	12	110.41	<0.0001
ppt	2	12	44.97	<0.0001
region*ppt	2	11.9	16.63	<0.001
distance	3	85.1	1.38	0.26
l. Soil C (log transformed)				
region	1	49.9	4.52	0.038
ppt	2	12.2	45.12	<0.0001
region*ppt	2	11.9	4.77	0.030
sand	1	52.3	9.90	<0.003
m. Soil N (log transformed)				
region	1	49.9	2.88	0.100
ppt	2	12.8	41.11	<0.0001
region*ppt	2	12.4	5.10	0.024
sand	1	53.9	13.28	<0.001
n. Soil bulk density				
region	1	63.8	2.10	0.15
ppt	2	14.3	40.62	<0.0001
distance	3	83.0	1.69	0.18
region*ppt	2	13.1	29.60	<0.0001
ppt*distance	5	82.3	1.97	0.091
sand	1	80.9	7.05	0.01

Appendix 4.2. F-tables for repeated-measures (2 years) mixed-model tests at specific study areas. “distance” refers to distance-from-water class, “radiation” is potential radiation based on slope and aspect, and “sand” is % sand in the surface soil.

Dependent variable & location	Independent variables	Num DF	Den DF	**F**	*p*
a. Perennial grass aboveground production (log transformed), arid Patagonian steppe (Río Mayo)					
	distance	3	16	0.07	0.97
	year	1	16	9.43	0.007
b. Palatable perennial grass aboveground production (log transformed), arid Patagonian steppe (Río Mayo)					
	distance	3	18	6.73	0.003
c. Shrub aboveground production (log transformed), arid Sagebrush steppe (Wanapum State Park)					
	distance	3	12	15.39	<0.001
	year	1	12	22.00	<0.001
	radiation	1	12	17.21	0.001
d. Shrub aboveground production (log transformed), semiarid Sagebrush steppe (Ellensburg)					
	distance	3	18	3.34	0.043
e. Shrub aboveground production (log transformed), arid Patagonian steppe (Río Mayo)					
	distance	3	17	0.047	0.71
f. Total aboveground production (log transformed), arid Sagebrush steppe (Wanapum State Park)					
	distance	3	14	3.93	0.032
g. Total aboveground production (log transformed), semiarid Sagebrush steppe (Ellensburg)					
	distance	3	16	3.59	0.037
	radiation	1	16	4.87	0.042
	sand	1	16	4.72	0.045
h. Total aboveground production (log transformed), arid Patagonian steppe (Río Mayo)					
	distance	3	17	0.29	0.83
	year	1	17	18.51	<0.001

Appendix 4.3. Plant species and species codes shown in the ordination figures.

Study area	Species code	Species name
Sagebrush steppe	agrspi	*Agropyron spicatum*
	arttri	*Artemisia tridentata v. tridentata*
	arttrip	*Artemisia tripartita*
	carfil	*Carex filifolia*
	fesida	*Festuca idahoensis*
	poacus	*Poa cusickii*
	poajun	*Poa juncifolia*
	poasec	*Poa secunda*
	sithys	*Sitanion hystrix*
	sticom	*Stipa comata*
	stiocc	*Stipa occidentalis v. nelsonii*
	stithu	*Stipa thurberiana*
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 spinossum*
	poalan	*Poa lanigunosa*
	poalig	*Poa ligularis*
	rhypic	*Rhytidosperma picta*
	senfil	*Senecio filaginoides*
	stihum	*Stipa humilis*
	stispe	*Stipa speciosa*

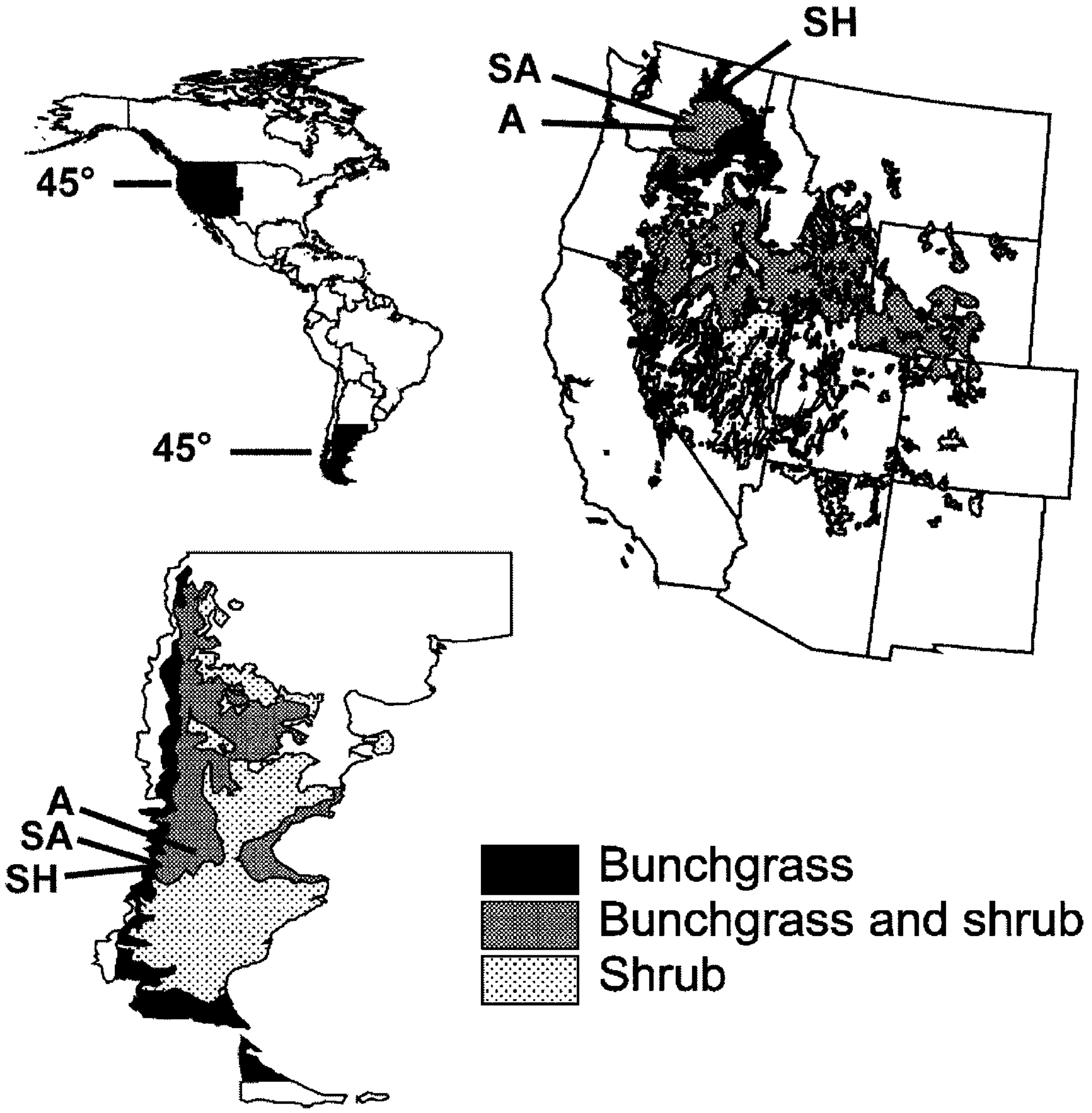

Fig. 4.1. Vegetation types and location of the arid (**A**), semiarid (**SA**), and subhumid (**SH**) study areas in the sagebrush steppe of North America and the Patagonian steppe of South America. For North America, the Bunchgrass area corresponds to Küchler's (1964) "Fescue/Wheatgrass" and "Wheatgrass/Bluegrass" vegetation types, the Bunchgrass and shrub and area is Küchler's "Sagebrush steppe," and the Shrub areas are mostly Küchler's "Great Basin sagebrush." For South America, the Bunchgrass area corresponds to León et al.'s (1998) "Subandean district," the Bunchgrass and shrub area to their "Occidental District," and the Shrub area to their "Central district."

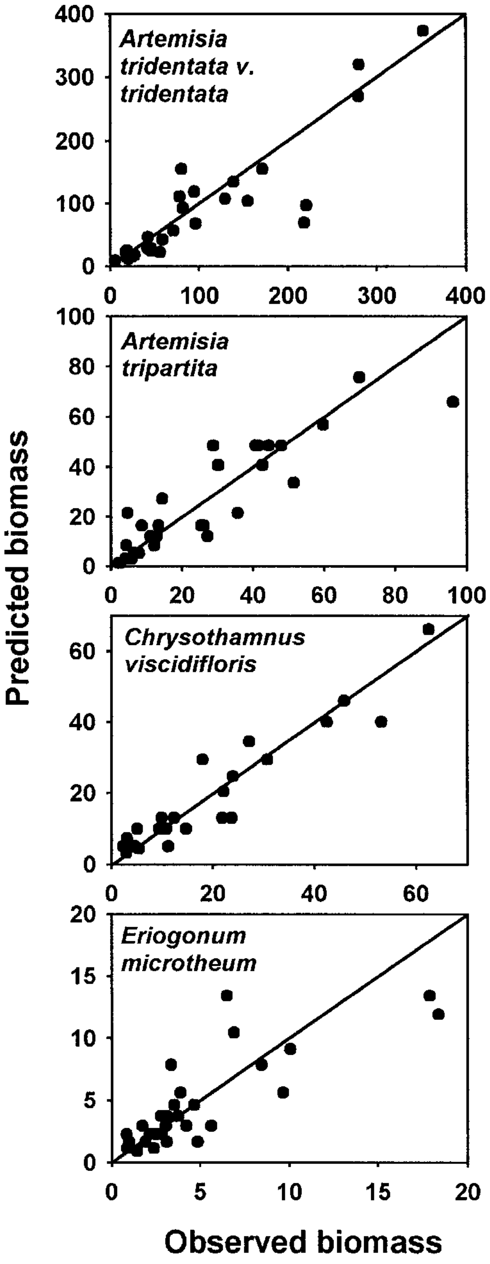

Fig. 4.2. Relationships between observed and predicted biomass for sagebrush steppe shrub species. The predictive models, model parameters, and r^2 values are shown in Table 4.4.

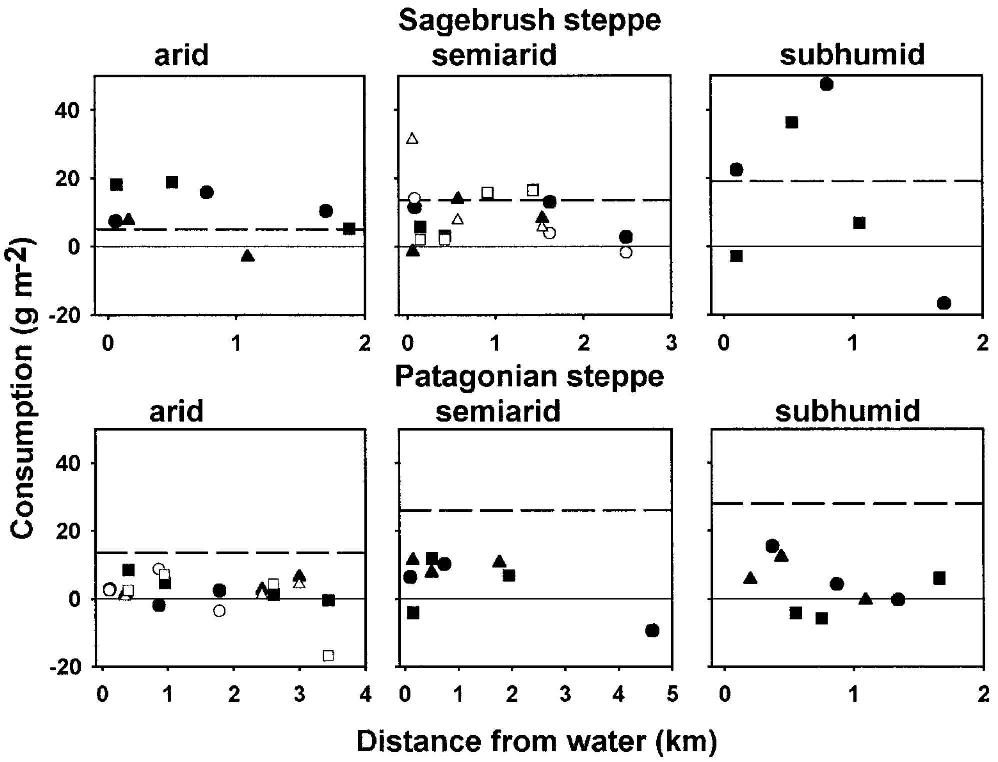

Fig. 4.3. The relationship between consumption (g m^{-2}), estimated by direct harvest, and distance from water at the six study areas. Different shaped symbols denote different transects within each study area, and hollow symbols show a second year of data. The dashed lines show expected consumption based on stocking rates. Negative values of consumption occur when forage biomass in the grazed area was higher than in the temporary exclosure, a result of spatial heterogeneity.

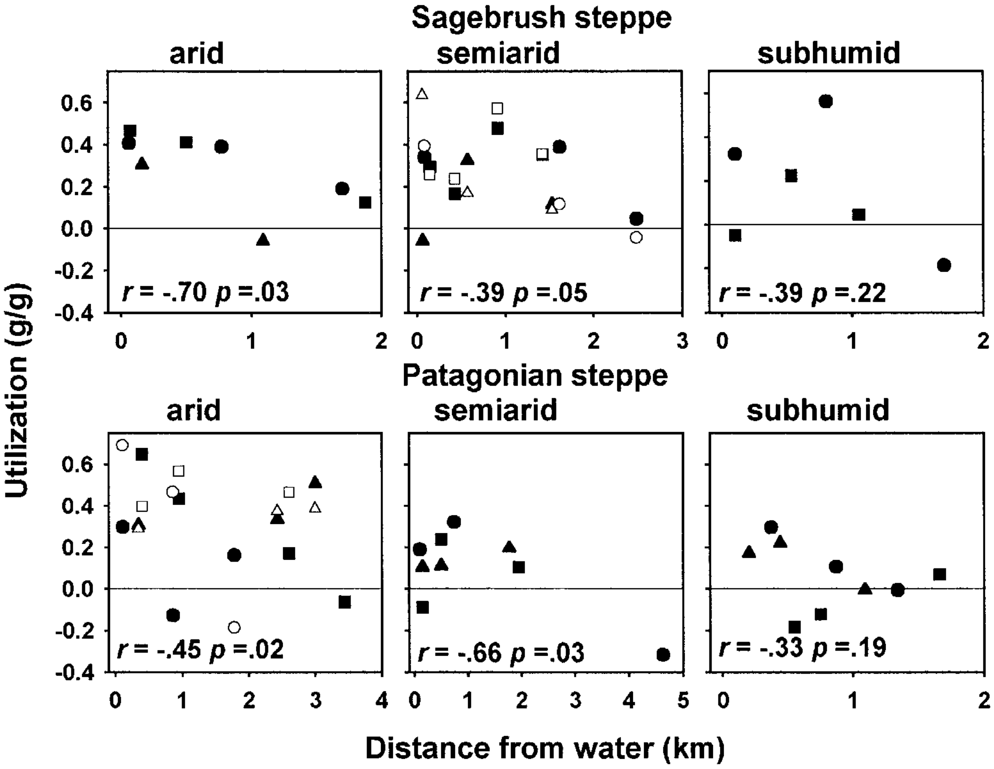

Fig. 4.4. Pearson's correlations (one-tailed tests) between distance from water and grazing intensity, defined as the proportion of forage production consumed, at the six study areas. Symbols are described in Fig. 4.3. Negative values of consumption occur when forage biomass in the grazed area was higher than in the temporary exclosure.

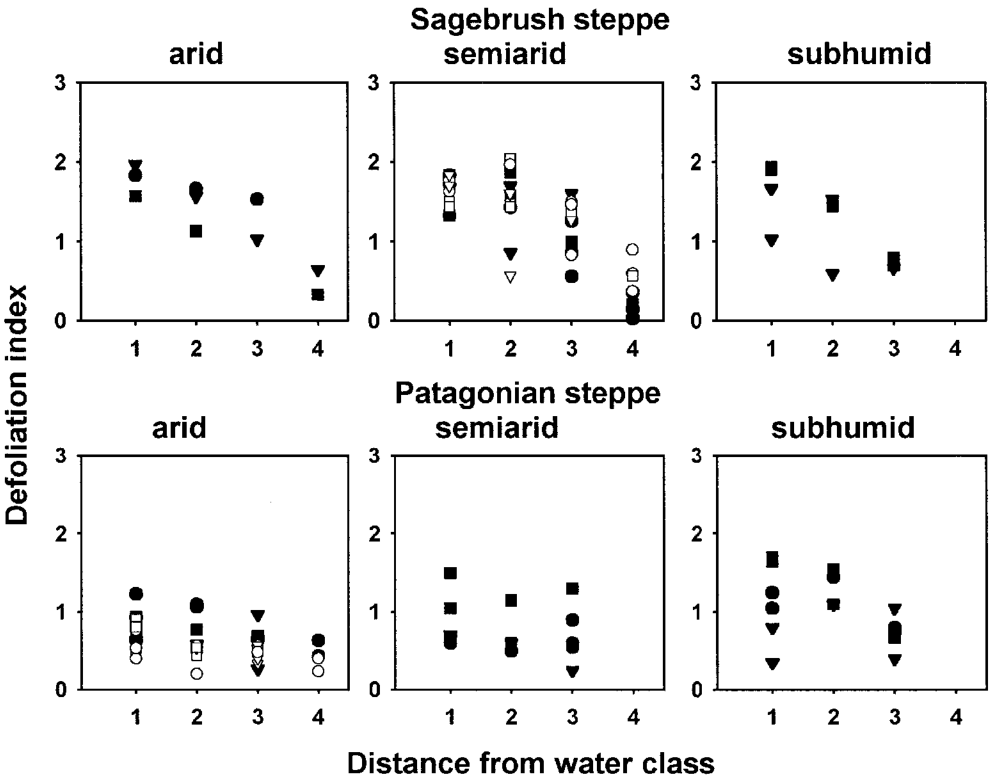

Fig. 4.5. Mean defoliation index by distance from water class at the six study areas. Symbols are described in Fig. 4.3. Long-term ungrazed sites correspond to distance class 4.

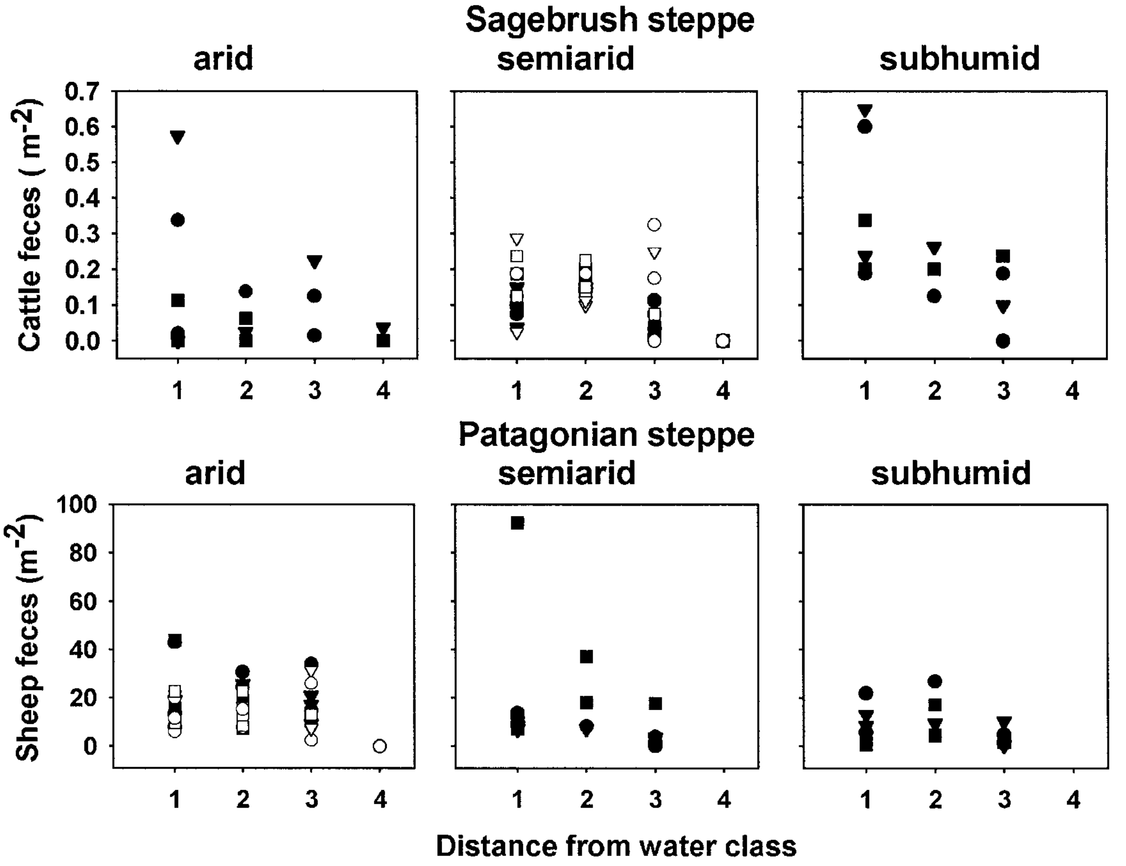

Fig. 4.6. The relationship between fecal counts and distance from water class. Symbols are described in Fig. 3. Distance class 4 refers to long-term ungrazed sites.

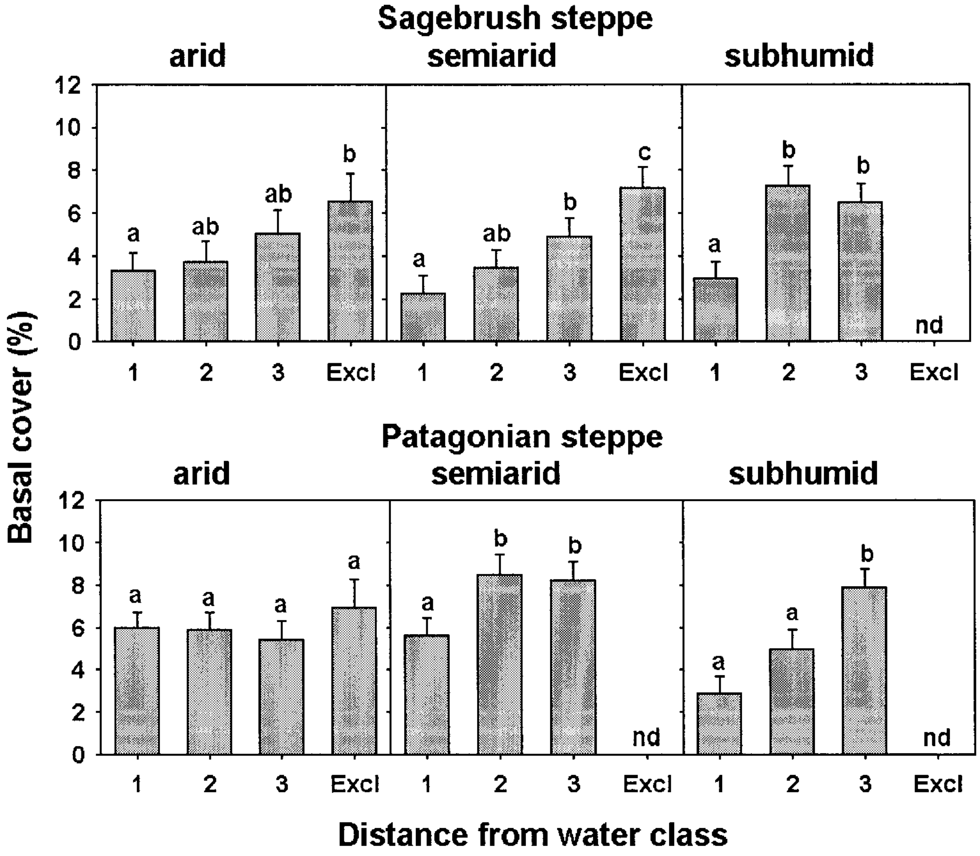

Fig. 4.7. Perennial grass basal cover as a function of region, precipitation, distance from water, and full interactions. Bars show standard errors, and least square means within each panel sharing lowercase letters are not significantly different ($\alpha = 0.05$). "Excl" refers to long-term ungrazed sites, and "nd" indicates no data.

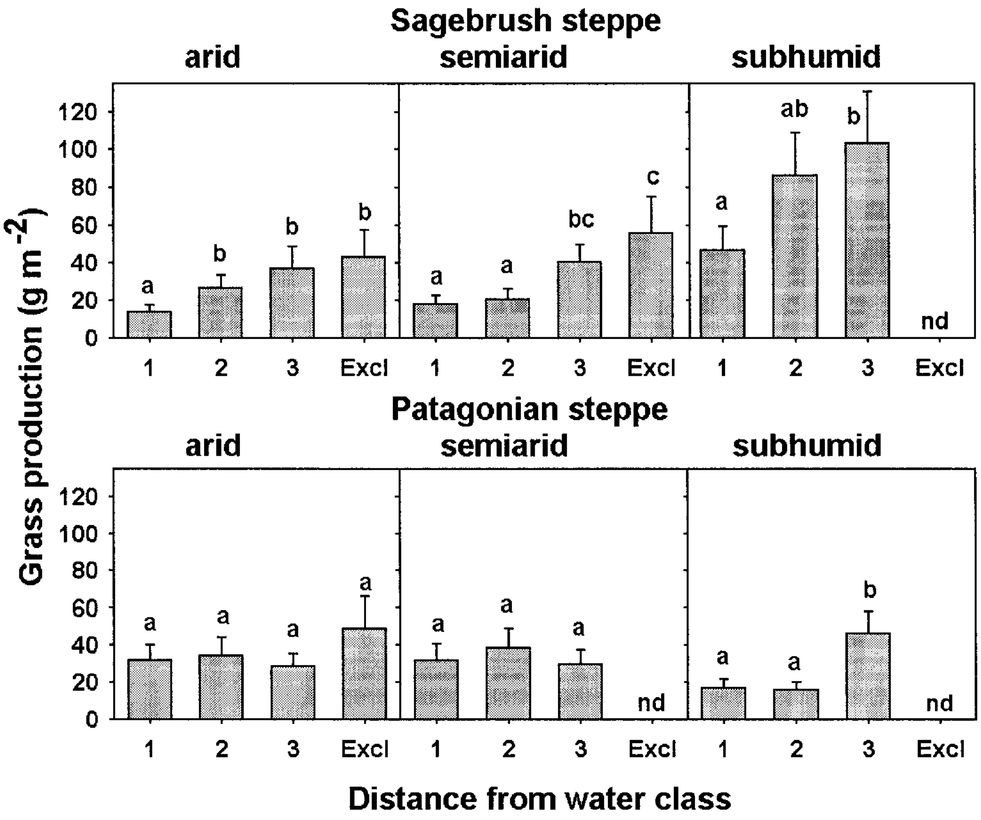

Fig. 4.8. Perennial grass production as a function of region, precipitation, distance from water, and full interactions. Bars show standard errors, and least square means within each panel sharing lowercase letters are not significantly different ($\alpha = 0.05$). "Excl" refers to long-term ungrazed sites, and "nd" indicates no data.

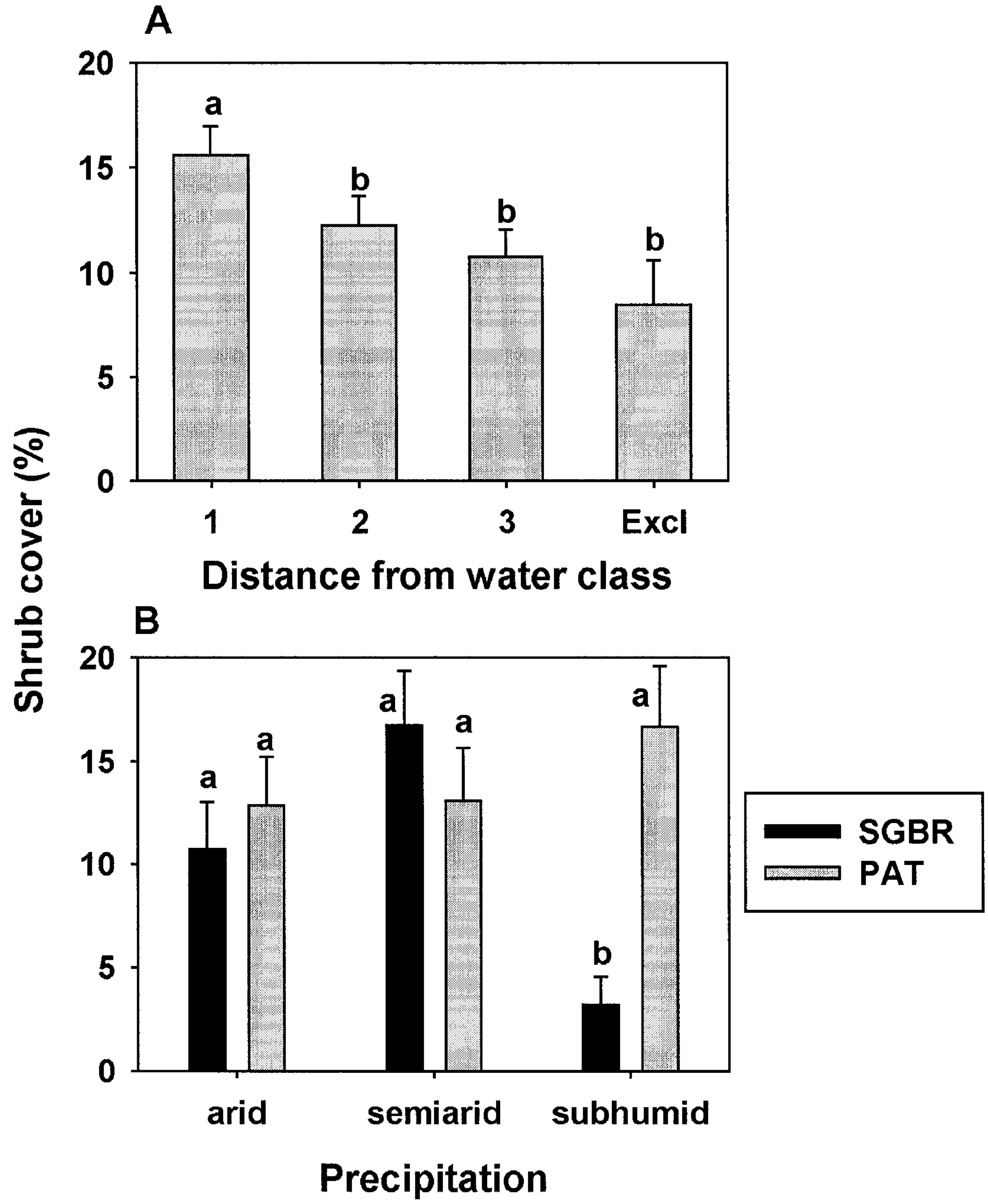

Fig. 4.9. The relationship between shrub canopy cover and **A**) distance from water and **B**) precipitation. Least square means within each panel sharing lowercase letters are not significantly different (α = 0.05).

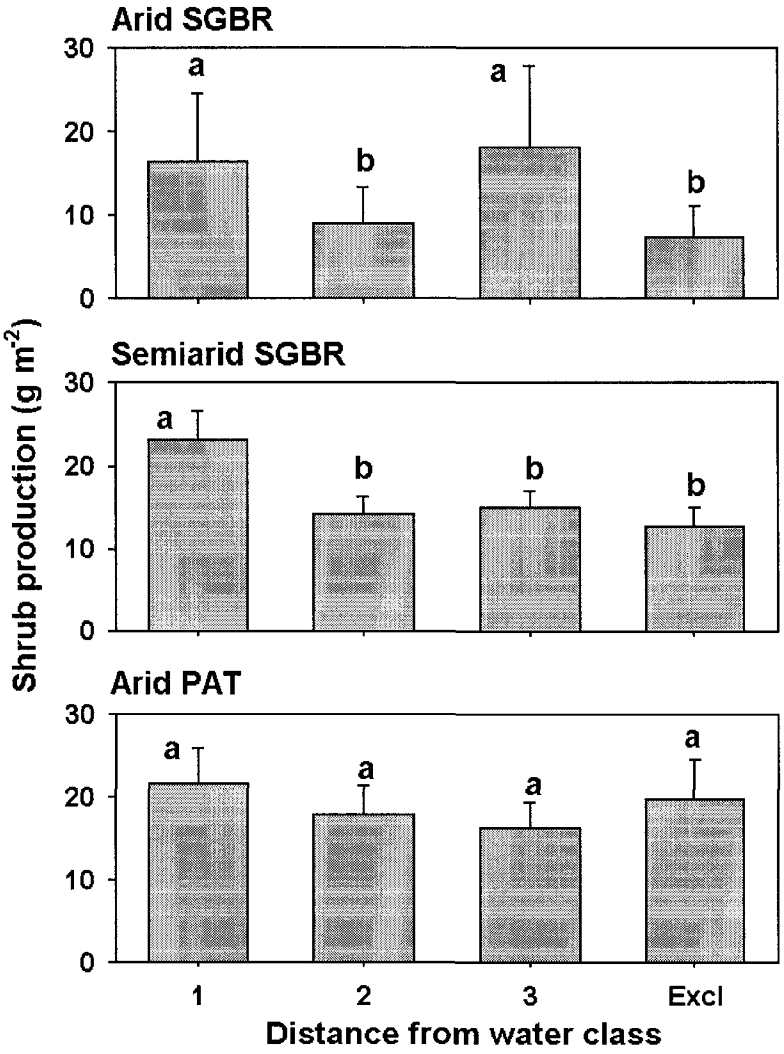

Fig. 4.10. Results of repeated measures (2 years) test of the effect of distance from water on shrub production at three study areas. Least square means sharing the same letter within each panel are not significantly different ($\alpha = 0.05$).

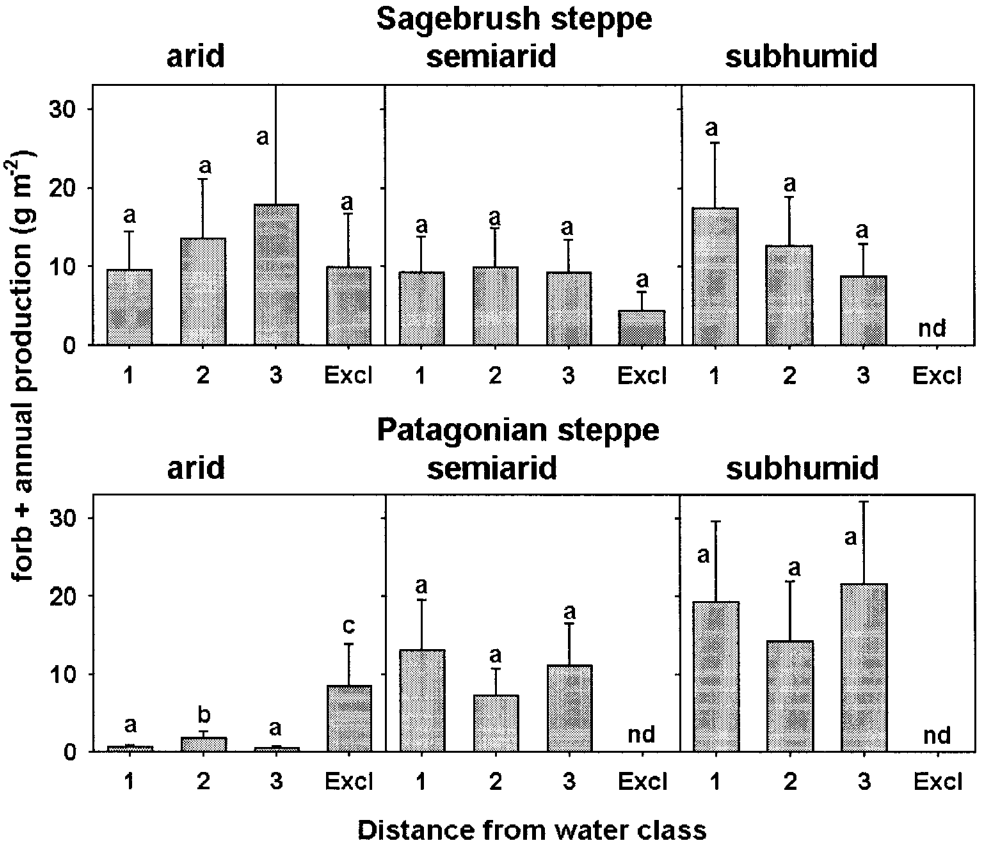

Fig. 4.11. Production of forbs and annuals at the six study areas. Least square means sharing the same letter within each panel are not significantly different ($\alpha = 0.05$). "Excl" refers to long-term ungrazed sites, and "nd" indicates no data.

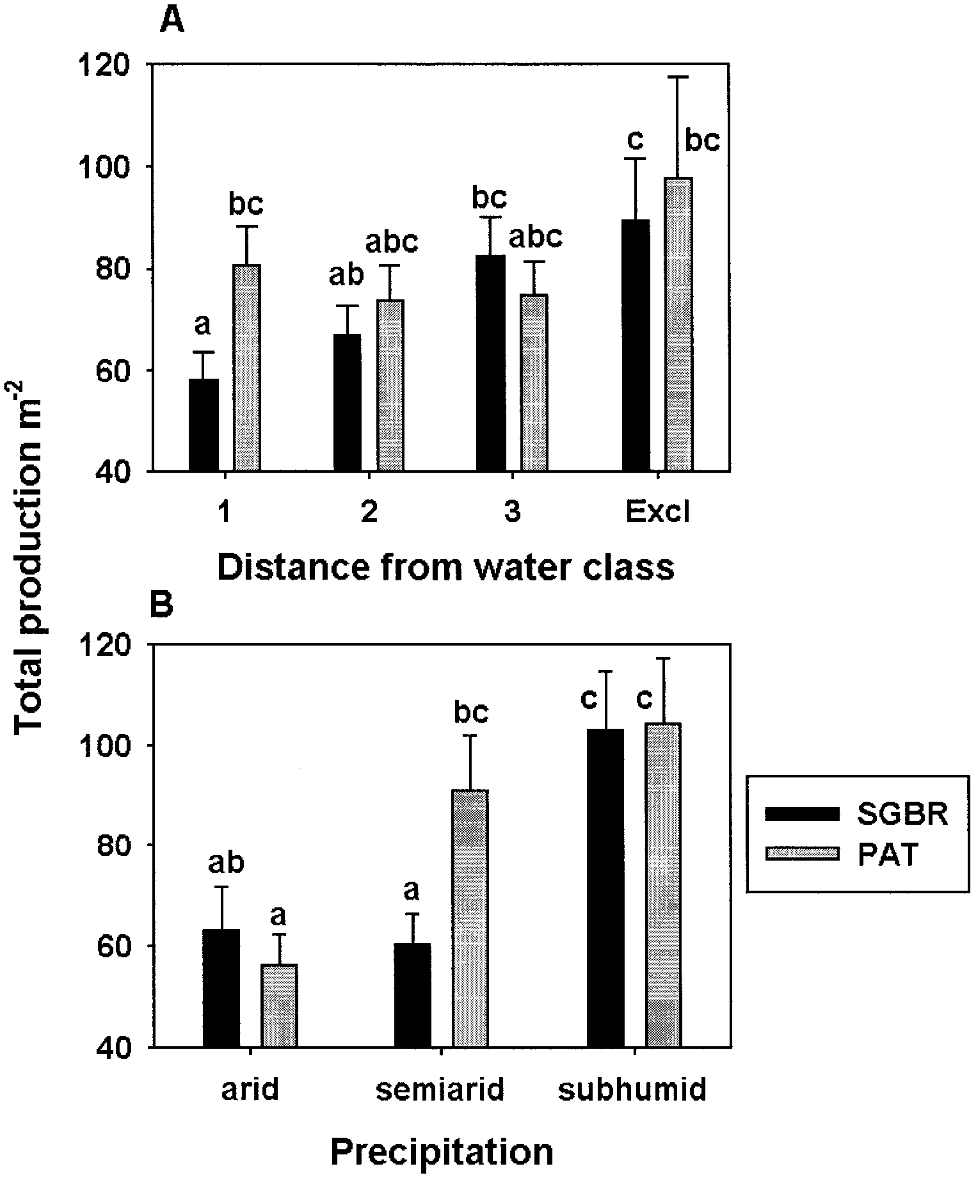

Fig. 4.12. Total production as a function of A) distance from water and B) precipitation. Least square means sharing the same letter within each panel are not significantly different ($\alpha = 0.05$). "Excl" refers to long-term ungrazed sites.

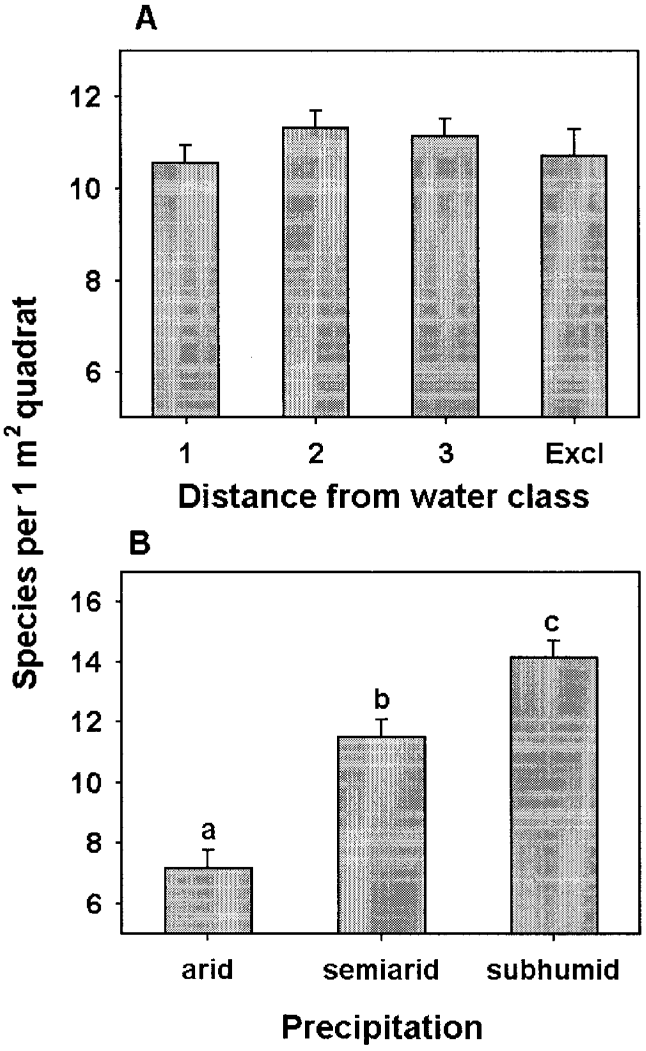

Fig. 4.13. Species richness per m^2 as a function of **A**) distance from water and **B**) precipitation. Differences among least square means in **A** were significant at $\alpha = 0.10$.

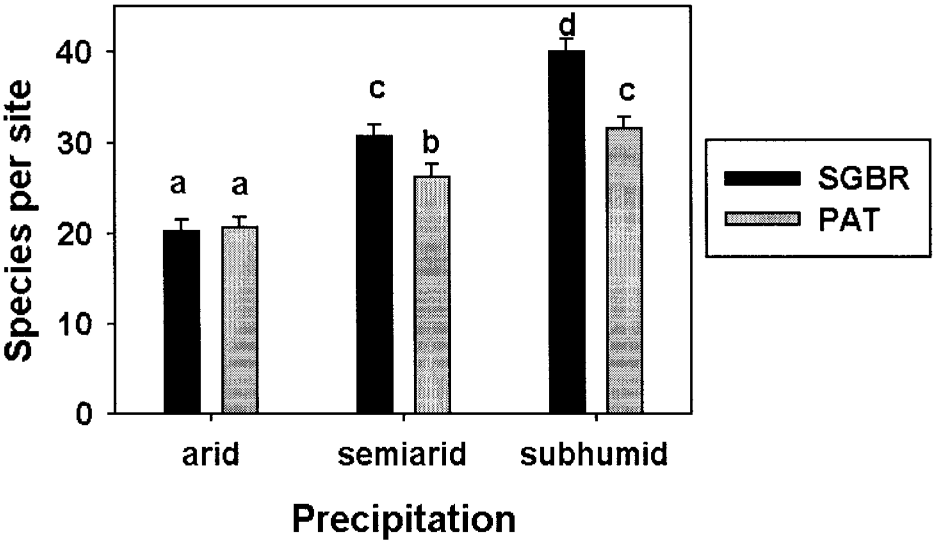

Fig. 4.14. Increases in species richness per site with precipitation in sagebrush and Patagonian steppe.

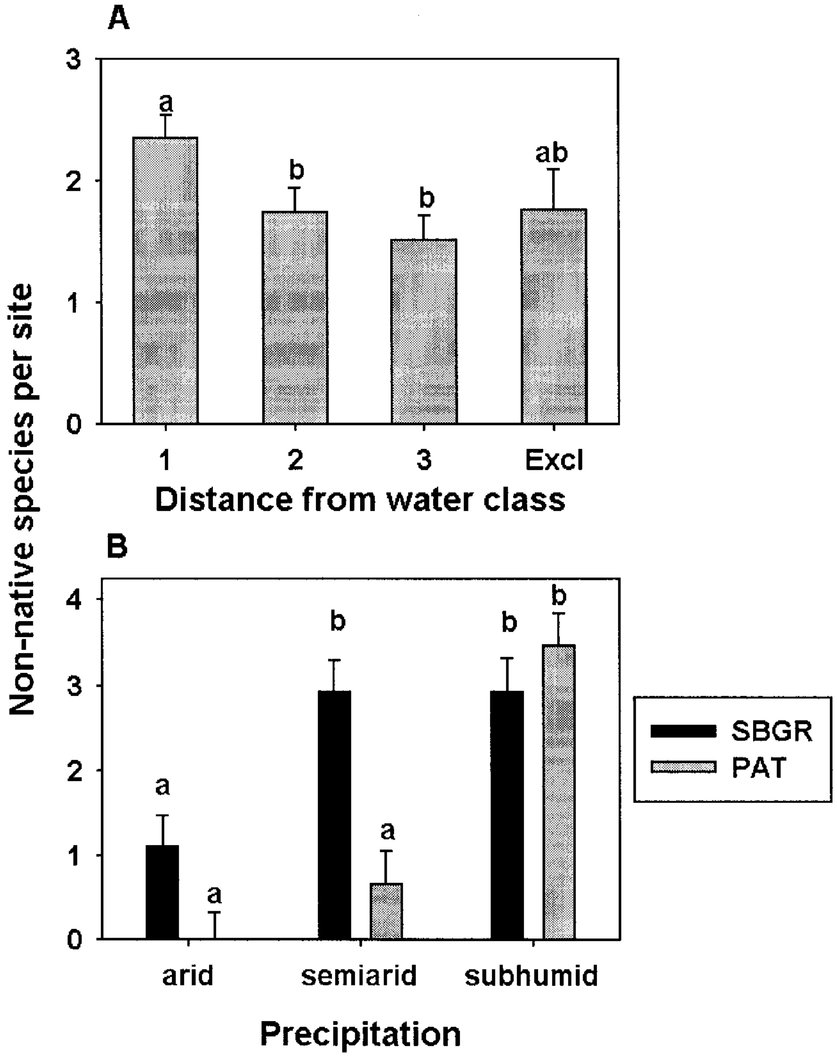

Fig. 4.15. Non-native species per site as a function of A) distance from water and B) precipitation.

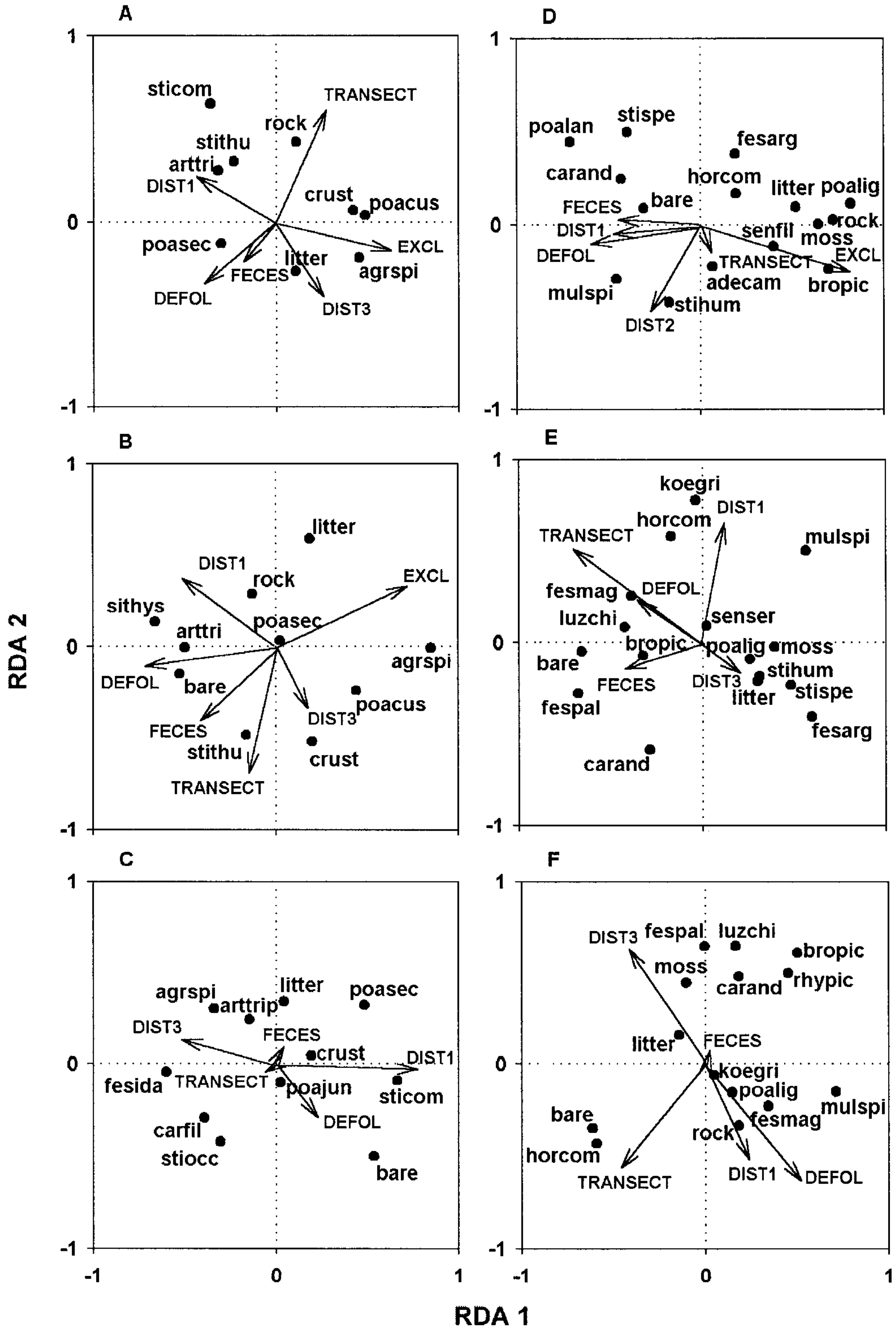

Fig. 4.16. Ordination results for arid, semiarid, and subhumid SGBR (**A-C**) and PAT (**D-F**) study areas. Locations in the plane RDA 1, RDA 2 of ground cover and important perennial grass and shrub species are shown by dots and labeled in lower case, while locations of grazing variables are shown by arrows and labeled in capitals. Species and grazing variables codes are described in Appendix 4.3.

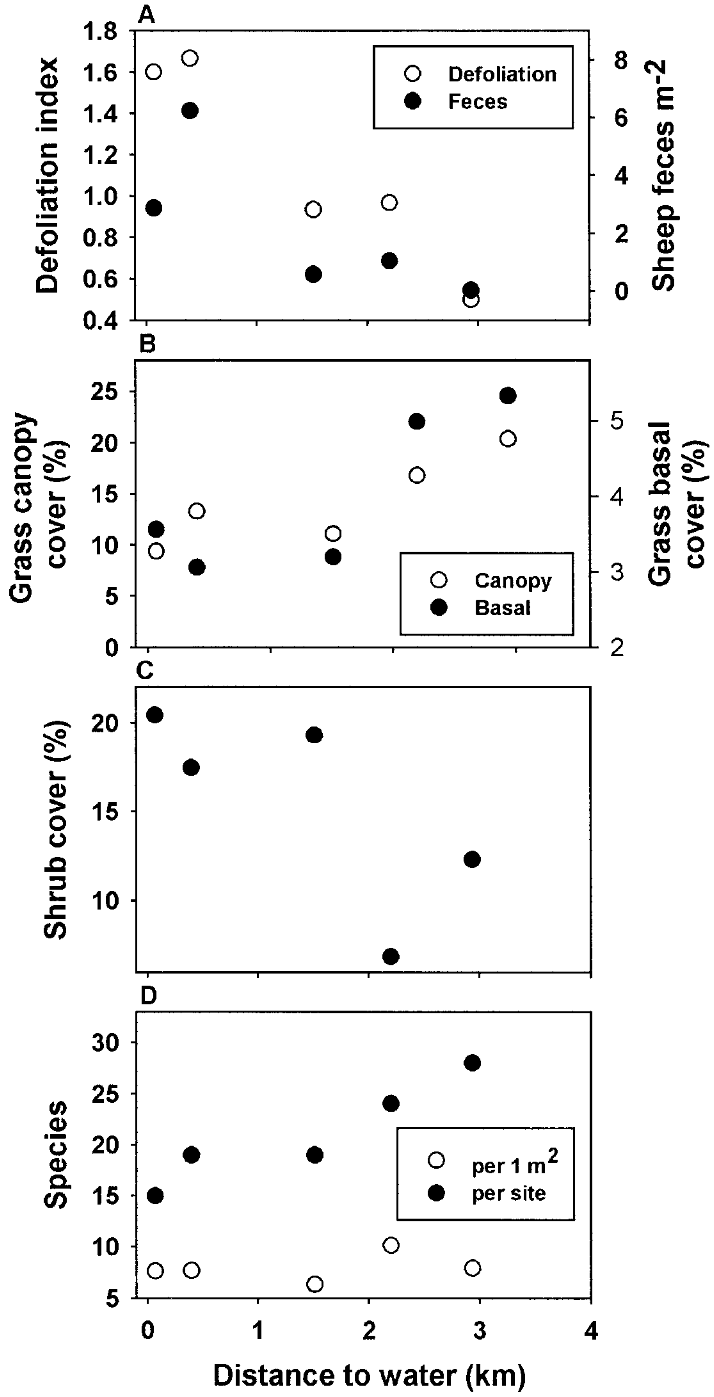

Fig. 4.17. Relationship between distance to water and defoliation index and fecal counts, perennial grass cover, shrub canopy cover, and species richness in one sheep pasture in sagebrush steppe.

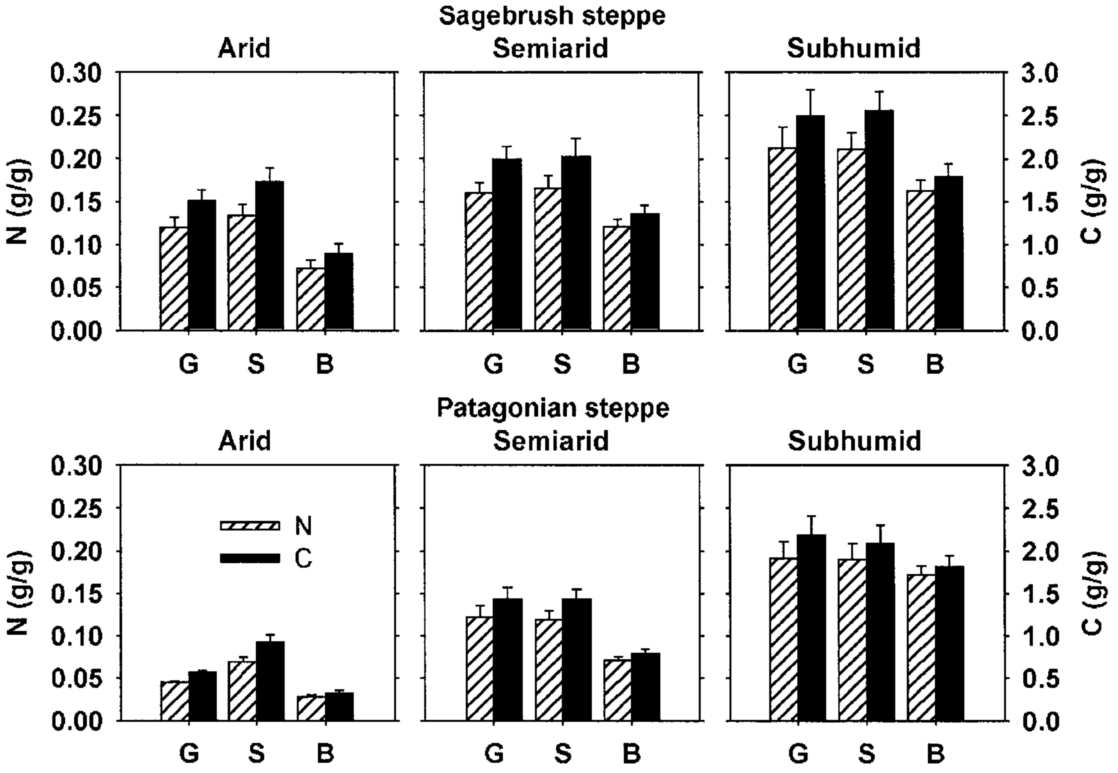

Fig. 4.18. Concentration of C and N in soils under grasses (G), shrubs (S), and bare ground (B) at the six study areas. Values shown are means and standard errors, aggregating sites across distance from water classes within each study area.

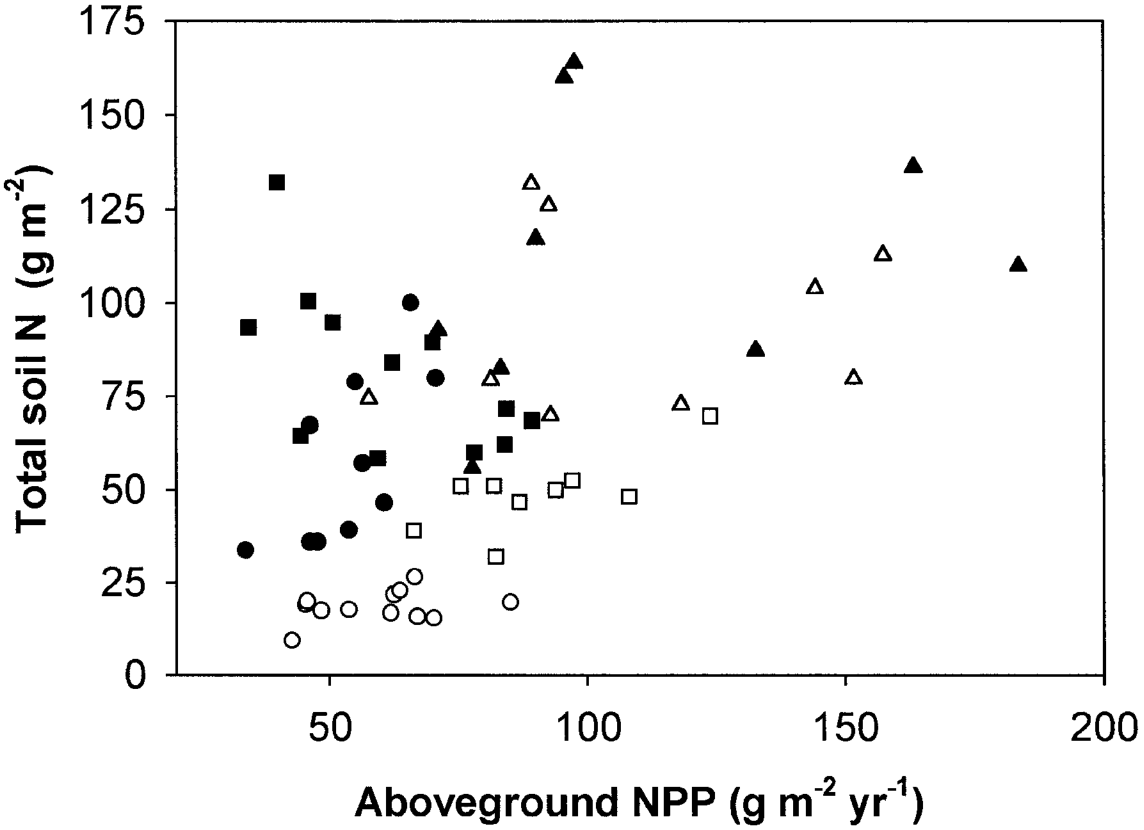

Fig. 4.19. The relationship between aboveground net primary production and total soil N in the top 5 cm at the six study areas. Solid symbols show SGBR study areas, open symbols show PAT. Different symbols denote arid (circles), semiarid (squares), and subhumid (triangles) study areas.

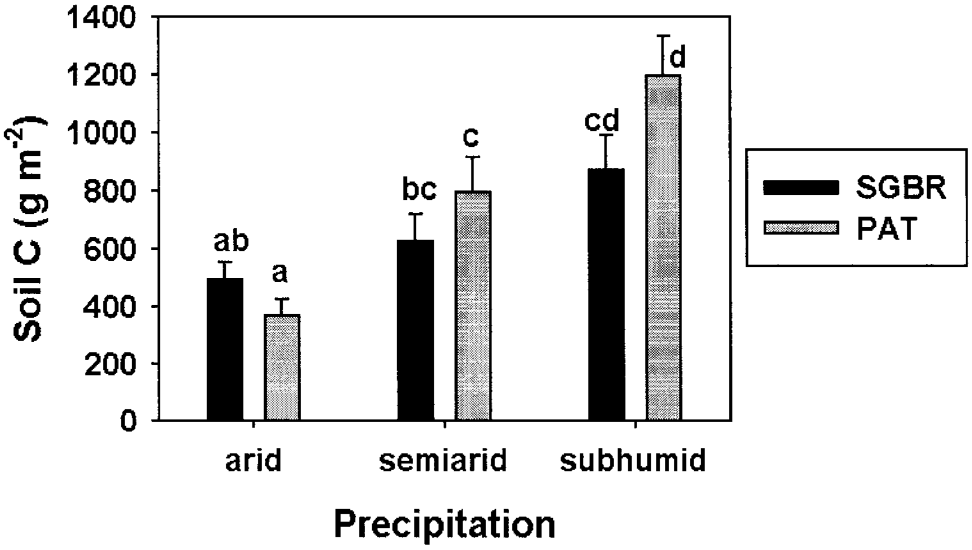

Fig. 4.20. Soil C in the top 5 cm as a function of precipitation. These least square means are based on a model that adjusted for differences in soil sand fraction among sites and study areas.

CHAPTER 5: CONCLUSION

My dissertation research represents two significant contributions to the literature. First, the sagebrush-Patagonian steppe comparison provided good evidence that plant functional traits determine the effect of grazing on plant communities. Second, although determining the origin of these differences in plant trait still requires separating the simultaneous and interacting selection pressures of evolutionary grazing history and abiotic factors, my research represents progress on this challenging question by identifying the critical plant traits and abiotic factors involved in conditioning the response of these ecosystems to grazing. In this chapter, I make the case for these contributions by reviewing the results from the individual components of the research, showing how they tie together to tell a larger story, and then outline their implications for future studies.

The comparison of abiotic factors (**Chapter 2**) showed how strong similarity in patterns of precipitation, past and present, and in geological history has created conditions for ecological convergence. But the comparison also demonstrated how small differences in soils and temperature could interact to create a longer growing season in Patagonia. In addition, the abundance of coarse textured soils in Patagonia suggests the potential for widespread areas of nitrogen limitation, at least relative to sagebrush steppe.

Functional traits of Patagonian graminoids differ from their sagebrush analogues in two important ways (**Chapter 3**): they tend to be shorter and of lower forage quality.

The forage quality of dominant plants at the arid Patagonian study area was particularly poor, compared to sagebrush steppe plants and plants from the subhumid Patagonian study area. The low quality of the dominant Patagonian plants will force grazers to be extremely selective in their foraging and may also limit secondary production, meaning low stocking rates compared to areas of sagebrush steppe with equivalent forage production. The results of the defoliation experiment suggest that, in a field context, tolerance may influence plant populations less than avoidance, further emphasizing the importance of traits related to forage quality.

Field sampling across gradients of grazing impact (**Chapter 4**) showed that consumption and utilization are lower in Patagonia than in sagebrush steppe. Based on foraging simulation models, the peaks in grazing intensity observed at intermediate distances from water probably developed after grazing decreased forage availability in locations near water (**Appendix I**). Decreases in cover and production of perennial grasses and increases in the abundance of shrubs near water sources was strongest in the sagebrush study areas, not significant in arid Patagonia, and moderate at the subhumid Patagonia study area. Grazing had only weak effects on species richness, and no significant effect on total soil C or N in either region. However, soil organic matter was much higher in arid sagebrush than arid Patagonian steppe, although there were no differences in soil organic matter between the subhumid sagebrush and Patagonian study areas.

The higher levels of consumption and utilization observed in sagebrush steppe explain the stronger effects of grazing on shrub and perennial grass abundance in this ecosystem relative to Patagonian steppe. In turn, the higher consumption in sagebrush steppe is a consequence of the higher quality forage of sagebrush steppe graminoids. Thus, differences at the level of plant traits, and especially those affecting forage quality, explain the contrasting response of sagebrush steppe and Patagonian steppe to grazing, and also explain differences within Patagonia. Graminoids in the subhumid Patagonian study area are richer in N than those in the arid study area, leading to higher levels of grazing intensity and larger impacts on the plant community.

While plant functional traits provide a proximate cause for differences in grazing response among these ecosystems and communities, identifying the ultimate cause requires understanding the origin of differences in plant traits. The evolutionary history of grazing offers one possible explanation: if dense herds of guanaco did exist in Patagonia, they would have exerted intense selection pressures on plants, leading to the evolution of short stature and poor forage quality as defenses against grazing. In contrast, plants in sagebrush steppe, where the density of native generalist grazers was lower, would have experienced weaker selection pressures. However, differences in abiotic factors lead to an alternative explanation: Patagonia's more extensive arid zone might have favored the evolution of xerophytic traits, and potential N limitation created by sandy soils could explain the low N content of the dominant grasses. Finally, the evolutionary history of grazing and these abiotic factors could have interacted. For example, N limitation may have favored the development of grazing resistance through avoidance, such as poor quality forage, rather than tolerance (Coley et al. 1985).

Understanding the root cause of differences in the response of sagebrush and Patagonian steppe to grazing therefore requires teasing apart the effects of evolutionary history of grazing and abiotic factors on plant traits. This problem lies at the forefront of evolutionary ecology (Thompson 1999), but my research can serve to outline at least the first steps in tackling the challenge by focusing attention on plant traits related to forage quality and on abiotic factors that can influence nitrogen availability. To guide future research, I describe two hypotheses and the predictions they generate.

The first hypothesis is that plant functional traits related to grazing avoidance explain grazing effects better than traits related to grazing tolerance. In other words, reduced palatability and poor forage quality are more important than the ability to replace leaf area lost to defoliation (Anderson and Briske 1995, Hendon and Briske 2002). Before testing this hypothesis, we need a better description of tolerance among grasses in these communities. *In situ* defoliation experiments at each of the study areas I used would be an excellent start, and experiments to quantify morphological plasticity within each species would be valuable as well. Once better information on tolerance is gathered, we can test the prediction that vegetation responses to grazing are more tightly correlated with avoidance traits than tolerance traits.

The second hypothesis is that plant functional traits related to grazing resistance are strongly influenced by abiotic factors such as soil texture. This hypothesis generates two testable predictions: first, forage quality will decrease with increasing soil sand content at patch and landscape scales in both sagebrush and Patagonian steppe, and under controlled conditions in the greenhouse, and, second, for plant species found in both ecosystems (such as *Stipa speciosa* and *Poa secunda*) but grown under common conditions, within ecosystem variability in phenotypes will be greater than between ecosystem variability. Systematic differences between sagebrush and Patagonian varieties of these species might suggest a greater role for the evolutionary history of grazing, or some other biological selection pressure. Better information on the phylogenetic histories of these species and genera (Grass phylogeny working group 2001) would aid the interpretation of these experiments.

The evolutionary history of grazing concept has influenced grazing research for more than two decades (Stebbins 1981, Mack and Thompson 1982, Milchunas et al. 1988). Is it still useful? After all, if our objective is to predict the current response of plant communities to grazing, then all we need is information on plant traits, as recent work including this dissertation demonstrates. However, we can never know if we have measured the critical plant functional traits, nor do we have data on plant traits in all ecosystems and communities where grazing is an important land-use. Furthermore, whether predictions based on plant traits apply to grazing effects on other taxa or on ecosystem properties such as nitrogen cycling is uncertain. The evolutionary history concept can serve as a qualitative predictor to patch these gaps in knowledge. But more importantly, even if plant traits can predict ecosystem responses to present grazing, they cannot explain the great variability among ecosystems. Plant traits themselves are legacies of abiotic and biotic selection pressures, including the evolutionary history of grazing. Understanding why different plant traits evolved in different ecosystems will require careful consideration of the role of evolutionary history of grazing and its interactions with climate and soils.

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APPENDIX I: SPATIOTEMPORAL PATTERNS IN FORAGE PRODUCTION AND UTILIZATION ALONG DISTANCE FROM WATER GRADIENTS

ABSTRACT

Large herbivores can impose spatial patterns on otherwise homogeneous vegetation, but how these patterns change through time is poorly understood. Domestic livestock pastures are model systems for studying how foraging behavior influences the evolution of coupled grazing and vegetation patterns. I sampled forage production and utilization by cattle along distance from water gradients to provide a "snapshot" of grazing and vegetation patterns, then tested the ability of simple simulation models to qualitatively reproduce these patterns. In the field, forage production increased with distance from water, as expected, but grazing intensity (utilization) peaked at intermediate distances from water. Likewise, simulations based on a variety of different foraging behaviors produced steep gradients in forage production and, after sufficient time, peaks in grazing intensity at intermediate distances. Distance from water gradients thus represent historical, but not necessarily contemporary, gradients in grazing intensity. The model with a foraging strategy based on time minimization produced more realistic patterns in forage abundance than models based on energy maximization. However, all models produced implausible thresholds in grazing and forage distribution, suggesting that factors besides resource distribution influence herbivore distributions. Moreover,

different foraging behaviors produced similar patterns, especially on point water source landscapes, demonstrating the difficulty of inferring process from pattern.

INTRODUCTION

Large herbivores can have strong effects not only on the mean abundance of plant species and functional groups, but also on their spatial distribution (reviewed in Adler et al. 2001). Grazing mediated changes in the spatial heterogeneity of vegetation can increase or decrease habitat diversity and, in turn, the diversity of consumer species (Smith 1940, England and DeVos 1969, Grant et al. 1982, Bock et al. 1984, Dennis et al. 1998, Matlack et al. 2001). This influence of large herbivores on overall biodiversity in grazing ecosystems raises the possibility of using grazers as tools for conservation management (Collins et al. 1998, Fuhlendorf and Engle 2001). In order to manage habitat diversity with grazers, however, we need a solid understanding of how large herbivores influence and respond to spatial heterogeneity. Although we can predict grazing's effect on spatial heterogeneity at one moment in time, given information on the spatial distribution of both vegetation and grazing pressure (Adler et al. 2001), the evolution of these patterns over time is poorly understood (Pastor et al. 1997).

Field studies provide limited and inconsistent information on temporal change in the spatial patterns of grazing and vegetation. In the tallgrass prairie of central North America, for example, the spatial dynamics of grazing and vegetation are driven by fire. Large herbivores preferentially graze recently burned patches (Hobbs et al. 1991, Pearson et al. 1995, Coppedge and Shaw 1998, Biondini et al. 1999), but the locations of such patches shift as new areas are burned. Burned patches are preferred for only 1-3 years after which they are avoided (Biondini et al. 1999). In contrast, heavily grazed patches in southern African grasslands do not shift over time, leading to severe localized degradation (Kellner and Bosch 1992). Similarly, differences in soil characteristics between heavily grazed patches and surrounding vegetation in Tierra del Fuego grasslands indicate that the patches are stable over time (Posse et al. 2000). Rigorous quantitative description of spatiotemporal patterns of grazing and vegetation would require long-term, spatially explicit data. Satellite imagery can provide these data at coarse scales (Jano et al. 1998), but intensive field sampling would be necessary at fine scales or for response variables that are difficult to estimate remotely.

Because collecting appropriate field data is so difficult, research on the evolution of grazing and vegetation patterns often must rely on simulation models. To study the reciprocal relationship between herbivores and vegetation over time, both herbivore foraging behavior and plant growth must be modeled in a spatially explicit format. This approach has successfully explained the development of vegetation spatial patterns in boreal forest browsed by moose (Pastor et al. 1999), the breakdown of vegetation patterns in grazed arid ecosystems (van de Koppel et al. 2002), and the grazing-forage quality feedbacks leading to patch grazing in grasslands (Hutchings and Gordon 2001, Morales in prep.). Farnsworth and Anderson (2001) used a taxis-diffusion model with coupled plant-herbivore dynamics to show how grazing can maintain persistent boundaries in a vegetation mosaic.

These models demonstrate that predicting the effect of herbivores on spatial heterogeneity requires a good understanding of their foraging behaviors (Farnsworth and Beecham 1999). Recent work on foraging behavior has emphasized two findings. First, herbivores make movement decisions based on factors operating at different spatial scales (Senft et al. 1987, Johnson et al. 2001). One of the challenges in modeling foraging behavior is assigning the proper weight to these different factors. When grazers optimize search efficiency at all scales, as under the marginal value strategy (Charnov 1976), they may extirpate food resources and endanger their own long-term persistence (Moen et al. 1998). On the other hand, if they are too restricted in their search, and ignore resource distribution at broad scales, they will fail to utilize available resources (Farnsworth and Beecham 1999). Adding a probabilistic element to the search can solve the former problem, while allowing foragers to respond to resource gradients can solve the latter (Farnsworth and Beecham 1999). Second, because forage biomass is often inversely related to digestibility (Coppock et al. 1983, McNaughton 1984), the instantaneous rate of digestible energy gain, a function of forage quantity and quality, may be highest in areas of intermediate biomass (Hobbs and Swift 1988). If large herbivores forage to maximize energy intake, then they should choose areas of intermediate over high biomass, as many empirical and modeling studies demonstrate (Wallis de Vries and Dalebroudt 1994, Wilmshurst et al. 1995, Hutchings and Gordon 2001, Fortin et al. 2003, Morales in prep.). On the other hand, if grazers base their foraging strategy on time minimization, rather then energy maximization, they should choose areas of high biomass (Bergman et al. 2001). The time minimization and energy maximization strategies will impose different spatial patterns on the landscape, but which strategy is most common remains unknown.

A principal challenge in empirical testing of foraging models is the complexity of natural landscapes. Therefore, we should attempt to apply models in simple settings such as piospheres, defined by Andrew (1988) as the zone of ecological impact surrounding a watering point in arid and semi-arid grazing systems. Piospheres are model systems for studying pattern evolution because vegetation develops clear, well-documented gradients as a function of distance to water, a classic example of large herbivores altering the spatial heterogeneity of vegetation (Andrew 1988, Huntley 1991, Pickup et al. 1998, Turner 1998, Ludwig et al. 1999, Nash et al. 1999, Thrash 2000). Furthermore, piospheres, especially in domestic livestock systems, are homogeneous, bounded, and easily replicated relative to more complex and open wild ungulate systems.

Despite these advantages, coupled plant-herbivore models have not been developed to study spatiotemporal patterns in piospheres. Weber et al. (1998) demonstrated that fine-scale spatial heterogeneity in grazing pressure has large consequences for vegetation in piospheres, but their model generated broad-scale heterogeneity by modeling defoliation intensity as a negative function of distance from water, making grazing distribution at this scale an input and not a response. Similarly, piosphere field studies have used distance from water as a proxy for stocking rate or grazing intensity, based on the assumption that grazing intensity, or utilization, decreases with distance from water (Andrew 1988, Pickup et al. 1998, Ludwig et al. 1999, but see Pickup and Chewings 1988). However, my direct measurements of consumption and utilization in piospheres of the sagebrush steppe in the northwestern U.S. conflicted with this assumption, and suggested that the distribution of grazing changes along with progressive changes in vegetation.

To explore the evolution of spatiotemporal patterns of vegetation and grazing in piospheres, I constructed a series of simulation models linking herbivore foraging behavior and vegetation dynamics. I used these models to address two questions: 1)

Under what conditions will peaks in grazing intensity develop at intermediate distances from water? 2) Can qualitative comparisons of simulated and observed vegetation patterns provide evidence for specific foraging strategies in livestock? More specifically, do time minimization or energy maximization strategies generate more realistic patterns?

METHODS

Field studies

I conducted fieldwork at three study areas spanning a range of mean annual precipitation in the sagebrush steppe of eastern Washington. Chapter 4 provides a detailed description of study areas, site selection, and field methods. The "arid" study area, located at Wanapum State Park near Vantage, WA (46.95°N, 120.01°W), receives approximately 170 mm annual precipitation, concentrated in the fall, winter, and spring, and has a mean annual temperature of 12°C. The primary vegetation type belongs to the *Agropyron spicatum-Artemisia tridentata* association (Daubenmire 1970), and is grazed every other spring by cattle. The "semiarid" study area, located just south of Ellensburg, WA (46.86°N, 120.42°W), also falls within the *Agropyron spicatum-Artemisia tridentata* association, but receives approximately 250 mm precipitation annually. Pastures at this study area are grazed every spring and summer by cattle. The "subhumid" study area above Grand Coulee, WA (48.00°N, 119.30°W) has a cooler, wetter climate, with a mean annual precipitation of at least 300 mm and mean annual temperature of 8°C. Vegetation at this study area belongs to the *Festuca idahoensis-Artemisia tripartita* association, and is grazed in spring-summer or summer-fall in alternate years.

I selected 3 to 4 sites along 3 distance from water gradients in each of these study areas. I used pastures in which stocking rate and the location of fences and water had remained relatively constant for at least 20 years. Each gradient originated from its own water source, though sometimes two gradients were located within the same pasture. Except for one gradient at the semiarid study area originating from a stream, all water came from point sources. Whenever possible, I took advantage of long term ungrazed control sites (> 20 years ungrazed) found on road verges or in ungrazed land adjacent to the grazed pastures. At each grazed site, I constructed a 10 x 10 m cattle exclosure. I used these exclosures to measure primary production in the 1 to 2 years following their construction, assuming that composition was identical to the adjacent grazed areas. Production was estimated by direct clipping both inside and outside the exclosures. Consumption was calculated as the difference between the grazed and ungrazed production estimates, and grazing intensity, or utilization, as consumption divided by ungrazed production.

Model development

I linked a vegetation submodel with an individual based herbivore foraging model. I ran simulations on two different landscapes: a circular landscape with a point water source, and a rectangular landscape with a linear water source. In both cases, I assumed that vegetation at time zero was homogeneous and that subsequent changes in vegetation caused by grazing were identical along any radius in the circular landscape or along any transect perpendicular to the water source in the rectangular landscape. This simplifying assumption allowed me to model these two dimensional landscapes in one dimension. The major difference between the two landscapes is that the area represented by each position along the distance from water gradient increases in the circular landscape. If each position x is separated by a distance of one, the areas represented by positions 1,2,3...x are 3.14, 9.42, 15.71...$\pi x^2 - \pi(x-1)^2$. In the rectangular landscape with a linear water source, each position represents exactly the same area, a strip parallel to the water source with area determined by the width of the pasture and the distance between each position on the distance from water gradient.

The vegetation model was composed of two species, or functional types: grass, the dominant competitor and the source of forage, and shrubs, which increase in biomass on sites where grazing decreases grass biomass. Shrubs are not consumed. I describe the dynamics of these species using a discrete time version of a Lotka-Voltera competition model:

$$\frac{dG_x}{dt} = \frac{R_G G_x (K_G - G_x - \alpha_S S_x)}{K_G} + m - \boldsymbol{c} \qquad \text{(Eq. 1)}$$

$$\frac{dS_x}{dt} = \frac{R_S S_x (K_S - S_x - \alpha_G G_x)}{K_S} + m - \boldsymbol{T} \qquad \text{(Eq. 2)}$$

where G_x is biomass of grass at position x, S_x is shrub biomass at position x, R_G and R_S are the instantaneous growth rates of grasses and shrubs, K_G and K_S are the grass and shrub carrying capacities, α_S is the effect of shrubs on grasses and α_G is the effect of grasses on shrubs. Consumption, $\boldsymbol{c}$, is a function of herbivore density and forage availability at position x, and trampling damage to shrubs, $\boldsymbol{T}$, is also a function of herbivore density at x. The small immigration rate m, identical for both species, prevents local extinction. Grass biomass at each position is updated with respect to losses to consumption as they occur, but changes in grass and shrub biomass due to growth and trampling are calculated only at the end of each day.

The main features of the foraging submodel are that every animal begins each day at the water source (position = 1) and then forages independently until meetings its daily intake requirement. At each position, the animal has to decide whether or not to take a bite of vegetation, based on a "start-eating rule." After removing one bite, the animal must decide which direction to move, based on a movement rule. In this respect my models differ from those in which an animal reduces the food resource in a patch to a certain level before moving. However, Farnsworth and Beecham (1999) showed that leaving a patch before it was depleted had few effects on model results, and Moen et al. (1997) found that animal fitness was higher when forage was only partially depleted in a cell.

I explored a series of models representing variations on the rules for making these decisions, and for determining the biomass removed with each bite. In the first model, animals attempt to maximize forage intake, a time minimization strategy. The second and third models incorporate different versions of an energy maximization strategy. The fourth model represents a null foraging strategy in which animals always move away from water. I explain implementation of the first model in detail and then, briefly, the variations introduced for the next three models.

The first model, and the one I used to explore the sensitivity of key parameters, is the time minimization model (TMin). Grazers in this model attempt to maximize their instantaneous rate of biomass intake. Since the time period of every foraging bout equals one, intake rate (g t^{-1}) and available intake (g) are equivalent. In this discussion I refer to the latter quantity. The start-eating rule is based on a comparison between available intake at the animal's current position and mean intake for the entire gradient. This rule assumes that animals have knowledge of resource conditions across the whole gradient, a good assumption for all but the first days after their introduction to the landscape. If available intake at the animal's current position is greater than a specified fraction of mean intake, the animal eats. If available intake falls below this threshold, the animal continues to move. Movement in this TMin model is also based on available intake. The animal compares the mean available intake within a specified perception distance in either direction, and then takes one step in the direction of greater mean intake with a probability p (the probability of making the correct decision).

I calculated available intake at each position, a function of biomass density, as

$$c_x = a(1 - e^{-bG_x}) \cdot t \quad \text{(Eq. 3)}$$

where c_x is the forage consumed by the herbivore in one bite at position x, G is grass biomass, and a and b are constants, and time, t, equals one. I interpret a as the maximum bite size, while b determines the slope of the function (Fig. I.1A). Available intake increases with biomass when forage is scarce, but then saturates at high levels of forage biomass. This function is a phenomenological form of Gross et al.'s (1993) mechanistic model for herbivore functional response. The model updates available intake every time a bite is taken.

Output variables are grass biomass, shrub biomass, consumption, and utilization at each position along the distance from water gradient, as well as the daily mean of distance traveled and bites taken for the population of simulated animals. The values of these variables are saved at specified time steps. Consumption and utilization are calculated over a specified time period: consumption is the sum of all intake at each position over this time period, while utilization is consumption divided by the sum of grass biomass at the start of the time period and all growth that occurred during the time period. Thus, values of consumption and utilization will increase with the length of the output period on which their calculation is based.

In the second model, animals attempt to maximize energy gain by basing their decisions on available intake divided by distance. This model is called the energy maximization distance model (EMax-Dist). The start-eating rule is unchanged from the TMin model, but movement takes into account distance from water: given a choice between equal available intake in either direction, the animal will choose to move towards water.

The third model, called the energy maximization quality model (EMax-Q) takes into account a trade-off between biomass quantity and quality. I incorporated the trade-off phenomenologically, by making available intake a quadratic function of biomass

$$c_x = \left(uG_x + vG_x^2\right) \cdot t \qquad \text{(Eq. 4)}$$

where c_x is available intake, now interpreted as available digestible energy, and u and v are constants (Fig I.1B). Both the start-eating rule and the movement rule are based on this measure of digestible intake, rather than available intake as in the previous models.

The fourth model, called the maximum distance model (MaxDist), uses the same start eating rule as the TMin model, but instead of making movement decisions based on available intake rates, animals always move away from the water source with the probability p.

Model simulations

I first ran a series of simulations to test the influence of various model parameters on the simulated patterns. I ran these simulations with the TMin model on both point and linear water sources landscapes and compared output at day 300, calculating consumption and utilization for periods of 50 days. To compare patterns generated by the different models, I ran each of the models on each landscape using constant parameter values (Table I.1). The landscapes were large enough so that animals never reached the end of the distance from water gradients. I chose vegetation parameters to reflect a dominant forage grass, and a less competitive unpalatable shrub. I chose the herbivores' maximum bite size and daily intake to approximate cattle, with values of 10 g (Gross et al. 1993) and 10,000 g (Morrison 1961) respectively. The probability of a correct move, the perception distance, and the start-eating threshold were set arbitrarily, after determining that their values had relatively little influence on the qualitative form of the simulated patterns. The number of herbivores had to be smaller in the linear water source landscapes because their effective size was small compared to the point source landscapes in which total area per position increased with distance from water. I ran each of these simulations to 500 days, outputting results every 50 days, except for the MaxDist model on the linear water source landscape, which I ran to 1000 days. Because the patterns resulting from different simulations using the same parameters were indistinguishable, all results shown are based on a single run for each model-parameter combination.

RESULTS

Field observations

Production of grasses, the dominant component of forage in sagebrush steppe, increased along distance from water transects in the arid, semiarid, and subhumid study areas (Fig. I.2). The form of the increase, however, was variable. On some gradients, production increased rapidly at distances close to water, but slowly further from water, while on other gradients production increased dramatically only at locations furthest from water or in ungrazed exclosures. When only the dominant forage species was considered (*A. spicatum* at the arid and semiarid study areas, and *F. idahoensis* at the subhumid study area), decreases in production near water were more dramatic (Fig. I.2). On at least one gradient in each study area, production of the dominant was close to zero at the location closest to water.

Consumption peaked at intermediate distance from water on the semiarid and subhumid gradients (Fig. I.3). Observed values of consumption tended to scatter around the pasture-wide expected consumption calculated from stocking rates. Utilization, the percent of available forage consumed, also peaked at intermediate distances along gradients at the semiarid and subhumid study areas (Fig. I.3). At the arid study area, utilization was highest close to water, and decreased with distance from water, though the difference in utilization between sites very near water and at intermediate distances was small (Fig. I.3).

Influence of model parameters on simulated patterns

Running the TMin model on a landscape with a point water source led to the rapid development of a gradient in grass biomass as a function of distance from water (Fig.

I.4A). Grass biomass was depleted down to the start-eating threshold at locations closest to water. At the outer edge of this degraded zone, grass biomass increased very rapidly, but the increase slowed as distance from water increased further, producing a concave-down curve. The tail of this curve gradually approached grass carrying capacity, which was maintained at distances from water never reached by the grazers. Increasing the number of animals increased the size of the severely degraded zone, and also increased the portion of the gradient affected by grazing, since animals had to walk farther to meet their daily requirement (Fig. I.4A). Increasing the daily intake requirement had little effect on the size of the degraded zone, but increased the length of gradient affected by grazing, because a higher requirement led to longer distances walked (Fig. I.4B). When the probability of correct movement decisions was high, the size of the degraded zone was small and the length of gradient visited by grazers long relative to simulations with lower probability of correct decisions in which animals were more likely to return to graze an already degraded location (Fig. I.4C). Changes in the perception distance used to make movement decisions had virtually no effect on the pattern of grass biomass (Fig. I.4D). Likewise, altering the parameter *b* that determines the slope of the functional response had only small effects on the pattern of grass biomass (Fig. I.4E). In contrast, smaller maximum bite sizes forced animals to travel further, decreasing the size of the severely degraded zone and increasing the length of gradient affected by grazing (Fig. I.4F). Increasing the start-eating threshold increased grass biomass within the degraded zone, but had little effect on the pattern on the rest of the gradient (Fig. I.4G).

Running the TMin model on a landscape with a linear water source also produced dramatic increases in grass biomass with distance from water, but the form of this pattern was distinct. As on the point water source landscape, grass biomass close to water was reduced to the start-eating threshold, but then biomass increased in a generally linear fashion until reaching carrying capacity at distances beyond the reach of the grazers (Fig. I.5). Increasing the number of animals increased the extent of the severely degraded area and the extent of the area affected by grazing at a given time step, and increasing daily requirement had a similar effect (Fig. I.5A,B). Increasing the probability of a correct move decreased the extent of both the severely degraded area and the area affected by grazing, and when the probability of grazing was equal to 1, grass biomass had not been reduced to the start-eating threshold by day 300 even at locations closest to water (Fig. I.5C). Increasing the perception distance had a stronger effect than on the point water source landscape. As perception distance increased, both the extent of the degraded area and the area affected by grazing decreased, similar to the effects of increasing the probability of a correct move (Fig. I.5D). Additionally, the pattern of grass biomass became extremely variable at fine scales. Increasing either b or the maximum bite size caused an increase in the extent of the degraded area, though varying maximum bite size had a stronger effect (Fig. I.5E,F). As in the point water source landscape, varying the start-eating threshold influenced biomass within the degraded zone, but had little effect on biomass along the rest of the gradient (Fig. I.5G).

The instantaneous growth rate of grass, R_G, had strong effects on the development of patterns in grass biomass and utilization. At low growth rates, decreases in grass biomass near water occurred rapidly and, in turn, utilization shifted away from water, producing a peak at an intermediate distance in both point and linear water source landscapes (Fig. I.6). At higher growth rates, grass biomass decreased more slowly close to water, shifts in utilization away from water occurred more slowly as well, and in some cases no intermediate distance peak in utilization developed (Fig. I.6).

Comparison of patterns generated by different models

On landscapes with a point water source, the TMin model generated a gradient in grass biomass that increased in extent with time: both the size of the severely degraded zone near water, and the portion of the landscape affected by grazing grew over time (Fig. I.7). Shrub biomass followed the opposite pattern, increasing with time, except for locations closest to water where trampling was severe. Further from water, grass competition kept shrub biomass low (Fig. I.7). Consumption was initially highest close to water, but this peak shifted away from water over time (Fig. I.7). Similarly, utilization initially decreased with distance from water, but then developed a narrow peak at an intermediate distance that shifted away from water over time (Fig. I.7). The MaxDist model produced virtually identical results to the TMin model. The EMax-Dist model, however, produced distinct patterns. As in the previous models, grass biomass was degraded down to the start-eating threshold close to water, but the growth of this zone over time was more rapid and the increase to carrying capacity at the outer margin of this zone much more abrupt (Fig. I.7). Shrub biomass, correspondingly, increased more rapidly and over a larger area (Fig. I.7). The peak in consumption shifted outward relative to the TMin and MaxDist models, and utilization developed a bimodal peak that shifted away from water with time (Fig. I.7). The EMax-Q model produced patterns quite similar to the EMax-Dist model: for grass biomass, a larger severely degraded zone and more abrupt increase to carrying capacity than the TMin and MaxDist models, a larger zone of high shrub biomass, a relative shift away from water in consumption, and a bimodal peak in utilization (Fig. I.I.7).

The evolution of spatial patterns over time was similar when the models were run on a landscape with a linear water source, but greater differences emerged between the patterns produced by each model (Fig. I.8). As on the point water source landscapes, all models showed the zone of low grass biomass and high shrub biomass increasing outward with time, although development of the severely degraded zone was slower compared to the point-source landscapes and there was a relative lack of trampling damage to shrubs in locations closest to water, because the linear water source landscapes did not concentrate grazers as intensely. Consumption again shifted away from water over time, accompanying an outward shift in utilization along with the development of a peak in utilization at intermediate distances from water. Whereas the TMin and MaxDist models generated similar patterns on the point water source landscape, on the linear water source landscape they generated very distinct patterns, with development of a severely degraded zone much slower under the MaxDist model (Fig. I.8). As on the point water source landscapes, the EMax-Dist and EMax-Q models generated similar patterns of grass and shrub biomass and consumption, but differences in the distribution of utilization emerged on the linear water source landscapes. Utilization developed a broad bimodal pattern in the EMax-Dist model, shifting away from water over time, but a narrower, single peak in the EMax-Q model.

With the decrease in forage biomass over time, animals were forced to take more bites and travel further to meet their daily intake requirements. Under the TMin model on a point water source landscape, the increase in bite number and distance walked was initially rapid, then slowed, whereas on a linear water source landscape, the increase in bite number and distance traveled accelerated with time, and the magnitude of the changes over time was much greater (Fig. I.9).

DISCUSSION

With respect to the first research question, I found that peaks in utilization at intermediate distances from water occurred in simulations based on a variety of foraging behaviors. Together with the observed data, these results suggest that distance from water represents historical gradients of grazing impact, but not contemporary gradients in grazing intensity. With respect to the second research question, the model using the time minimization strategy produced more realistic patterns in forage abundance than models based on energy maximization. However, all models produced implausibly abrupt changes in grazing and forage distribution with distance from water, suggesting that factors besides resource distribution influence herbivore distributions. Furthermore, that different foraging behaviors produced similar patterns demonstrates the difficulty of inferring process from pattern.

Evolution of grazing intensity

While the development over time of peaks in consumption at intermediate distances from water should be expected, since high consumption requires both grazing pressure and high forage availability, the standard piosphere concept assumes that utilization, which is not related to forage availability, decreases monotonically with distance from water. However, both my field observations and models run on point and linear water source landscapes generated patterns of utilization that peaked at intermediates distances from water. My field data are unique, since most piosphere field studies used distance from water as a proxy for grazing intensity and included no direct measurements. However, available data on livestock densities across such gradients provide further evidence for intermediate peaks in grazing intensity. Pickup and Chewings (1988) showed that observed and modeled cattle densities peaked at intermediates distances in semi-arid Australian piospheres. Turner and Hiernaux (2002) estimated livestock density around villages in sub-Saharan Africa and also found that densities were highest at intermediate distances.

The simulations demonstrated that the intermediate peak in utilization does not develop until forage abundance is decreased to very low levels close to water. Altering the variables that influence the rate of degradation, such as stocking rate, maximum bite size, and the growth rate of grasses, can slow down or prevent the development of the intermediate peaks in utilization. Because forage availability near water decreases more rapidly on point than linear water source landscapes, the intermediate peak in grazing intensity develops sooner, and because the ultimate extent of the degraded area is larger on the linear source landscapes, the peak in grazing intensity shifts further from water.

These results suggest that when grazers are first introduced to a new pasture with uniformly high forage abundance, or in pastures where grazers never cause dramatic changes in forage abundance, we should expect grazing intensity to decrease with distance from water, as piosphere field studies often assume. Once forage abundance has been reduced to very low levels near water, however, we should expect peaks in grazing intensity at intermediate distances. Distance from water thus represents a gradient in historical or cumulative grazing intensity, but not necessarily a gradient in current grazing intensity. Distance from water gradients are appropriate proxies for grazing pressure for studies focused on the long-term effects of grazing, but not for studies aimed at measuring the effects of current grazing intensity.

Simulation over longer time scales showed that the intermediate peak in utilization persisted, but continued to shift away from water and gradually decreased in magnitude. However, my models cannot be expected to provide reliable results on such long time scales for two reasons. First, because I did not model herbivore energetics, changes in forage abundance have no feedback on the grazer population in my models. In reality, as forage availability declines with time, the grazers must walk further and further to satisfy their daily requirements. At a certain point, this increase in energy expenditure will have consequences for individual and population growth. In domestic livestock pastures, this typically translates into a decreased stocking rate or decreased reproductive rates (Paruelo and Sala 1992, Golluscio et al. 1998). Therefore, the expansion over time of the degraded area near water that my models generate cannot continue indefinitely. The second reason my models should not be used to simulate long-term patterns has to do with my use of the standard Lotka-Volterra equations for vegetation growth and competition. Plant growth in most grazing systems is seasonal, and while the Lotka-Volterra approach may approximate vegetation dynamics during the growing season, how defoliation affects growth the following season is more complex. For example, field studies show that a plant's ability to recover the season following a severe defoliation event depends on the timing of defoliation (Blaisdell and Pechanec 1949, Ganskopp et al. 1988). Modeling patterns of forage production over the long-term would require a better understanding of these interannual dynamics.

Time minimization or energy maximization?

All models run on the point water source landscape produced patterns with extremely abrupt thresholds in plant biomass, consumption, and grazing intensity. Adding area-restricted search (Stern 1998, Fortin et al. 2003), which allows animals to move quickly through areas of low forage availability and more slowly through areas of high forage abundance, had little effect on patterns generated by the TMin model (not shown). Although the form of the grass biomass patterns are quite similar to the logistic model proposed by Graetz and Ludwig (1978), the steepness of the ascending portion of the curves seems unrealistic. While some of the piospheres surveyed by Graetz and Ludwig do demonstrate steep transitions, most field data, including my own, show gradual changes in plant or forage biomass with distance from water (Graetz and Ludwig 1978, Pickup and Chewings 1988, Pickup et al. 1994). Patterns simulated by the EMax-Dist and EMax-Q models produced especially steep thresholds, while the TMin model did somewhat better, suggesting that energy maximization may be less common in natural systems than time minimization strategies, as a recent field study suggests (Bergman et al. 2001).

The implausible transitions my simulations produced indicate that other factors not included in the models have important influences on animal movement. In my models, animal distribution is controlled exclusively by the location of water and forage availability. As a result, when my simulated grazers are introduced to a pristine, homogeneous, landscape, they will graze close to water until they deplete forage biomass and are forced to disperse. The exception is the MaxDist model, but the fact that this model also produced steep thresholds in forage biomass, at least on the point source landscape, suggests that unknown factors causing the animals to disperse away from water must be strong to overcome the geometric constraint.

Field studies have identified influences on animal movements that my models ignored. Armstrong and Robertson (2000) found that the need for shelter from harsh winter weather had a strong effect on sheep distributions in U.K. hills. Similarly, deer selected habitat based on proximity to forested shelter (Mysterud et al. 1999). Social dynamics, inevitably an important factor in herds, can constrain patch choice and, in one modeling study, influence intake rates and resource variability (Beecham and Farnsworth 1998). Including the information that herbivores gain and lose as they forage may also influence foraging (Beecham and Farnsworth 1998). If these factors compel animals to explore distant areas of the pasture, even when forage is available closer to water, then models including them might generate smoother, more realistic patterns of vegetation and grazing.

Inferring process from pattern

Simulations with different foraging strategies on landscapes with point and linear water sources showed how the effects of geometry can dominate those of behavior. On the point water source landscapes, the TMin model and the MaxDist model, in which animals always move away from water, produced virtually identical spatiotemporal patterns of grass and shrub biomass, consumption, and utilization. The concentration of animals around water was so intense, and the development of steep gradients in forage availability so rapid, that maximizing intake, the search strategy in the TMin model, required moving away from water in almost every case. In contrast, on the linear water source landscape, in which animals were not so intensely concentrated and gradients in forage availability developed more slowly, the two models produced quite different patterns. Under the TMin model, animals moved out of the degraded zone close to water, but once they reached areas in which available biomass was at its maximum, their movement became a random walk. Under the MaxDist model, they continued to move away from water even after reaching areas that provided them with the maximum bite size. As a result, grazing impacts were spread over a larger area in the MaxDist model and severe degradation was much slower to develop. The geometric constraint, so strong on a landscape with a point water source, was relaxed on the linear water source landscape, allowing different behaviors to produce contrasting patterns.

On both point and linear water source landscapes, the two energy maximization models generated similar patterns. Both of these models provide an incentive for animals to stay closer to water. The EMax-Dist model achieves this by forcing animals to move closer to water when intake rates in either direction are equal. The EMax-Q model achieves this by assuming that areas with high biomass offer poor forage compared to areas with moderate biomass. Areas of high biomass tend to be further from water, and animals will choose to forage in previously grazed, lower biomass areas nearer water. As a result, patterns of forage biomass produced by these model show abrupt thresholds at the interface between grazed and ungrazed portions of the gradient, rather than the smoother transition typical of the TMin model.

That different foraging strategies can produce similar patterns, whether because of geometric constraints or the correlation between distance from water and forage quality, underscores the difficulty of inferring process from pattern. Data on animal movements, patterns of plant biomass, or grazing pressure may not be sufficient to allow clear determination of the factors influencing animal movement. By gathering such data on a variety of different landscapes, however, we may improve our ability to identify the true mechanisms.

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Table I.1. Parameter values used in simulations comparing different foraging behaviors on different landscapes.

Parameter	Description	Value
Landscape structure		
L	Length of distance from water gradient (m)	3000
W	Width of linear water source pastures (m)	200
d	Distance between each position on the gradient (size of cells) (m)	1
Vegetation		
K_G	Grass carrying capacity (g)	100
K_S	Shrub carrying capacity (g)	100
R_G	Grass maximum growth rate (g/g)	0.02
R_S	Shrub maximum growth rate (g/g)	0.01
α_G	Grass competition coefficient (g/g)	0.8
α_S	Shrub competition coefficient (g/g)	0.2
m	Immigration (g)	0.001
T	Trampling damage (g)	0.001
Herbivores and foraging		
N	Number of herbivores in point / linear water sources landscapes	50 / 10
DR	Daily required intake (g)	10,000
ET	Start-eating threshold (fraction of mean intake)	0.2
p	Probability of correct movement decision	0.9
PD	Perception distance (m)	1
a	Maximum bite size in MI, MD, and MID models (g)	10
b	Shape of functional response in MI, MD, and MID models	0.1
u	First parameter for functional response in DI model	0.35
v	Second parameter for functional response in DI model	-0.003

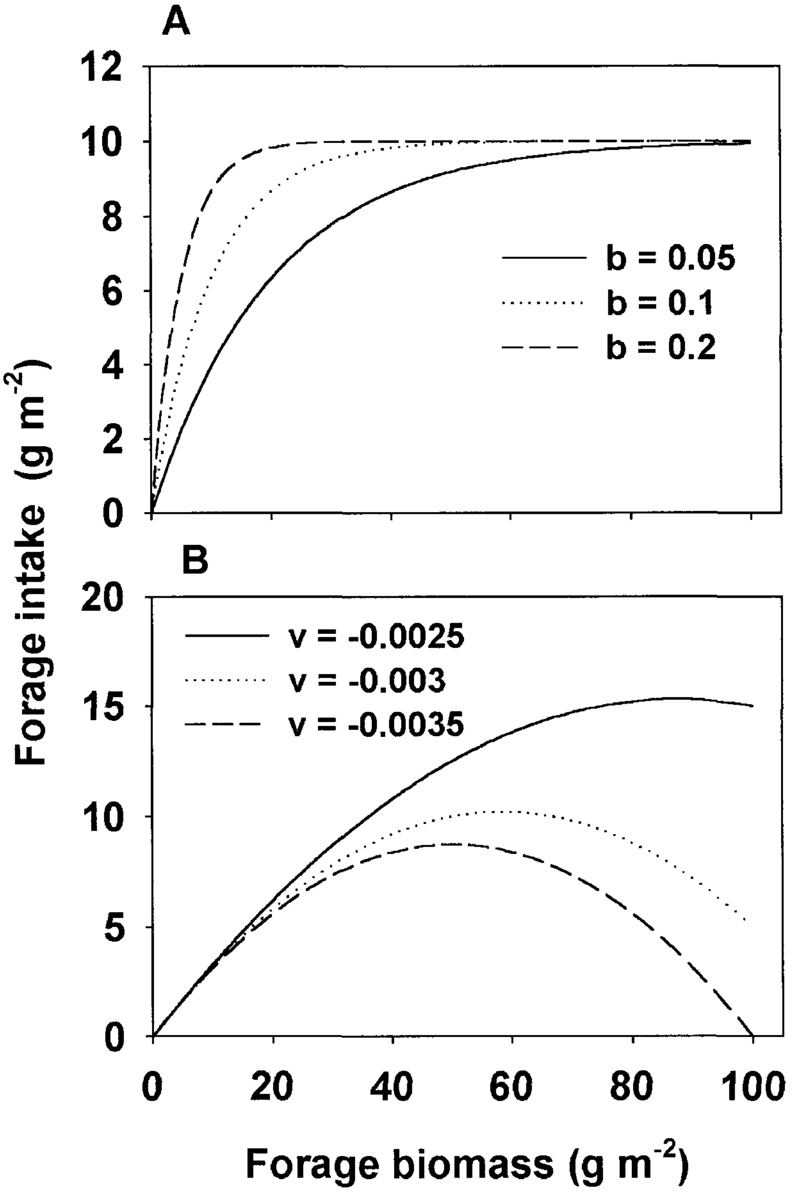

Fig. I.1. The relationship between forage biomass and forage intake per bite in A) the maximum intake model (Eq. 3) and B) the digestible intake model (Eq. 4) for various values of the parameter controlling the shape of the functional response.

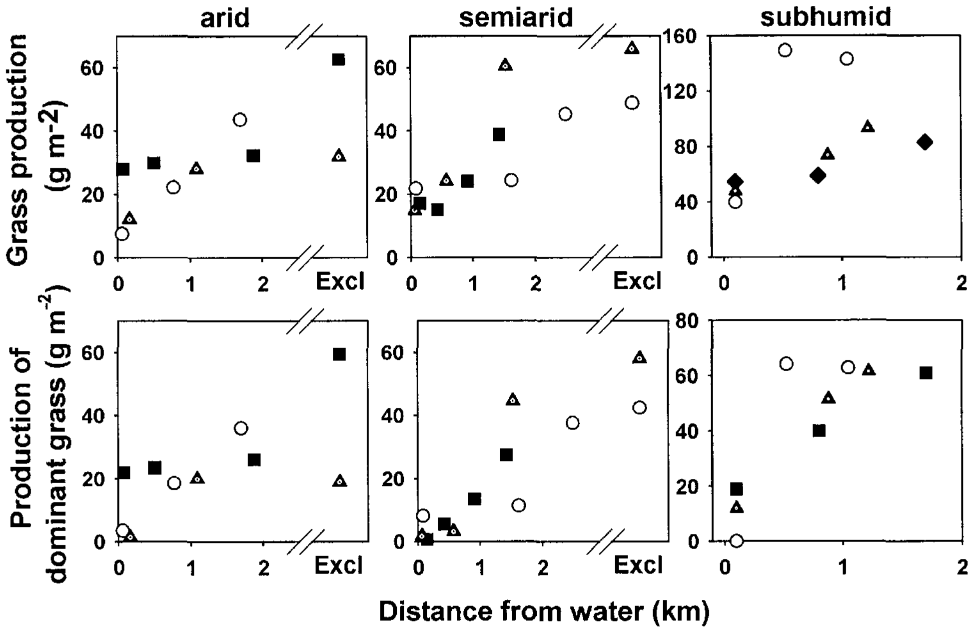

Fig. I.2. Production of grasses, the dominant forage species, along distance from water gradients in arid, semiarid, and subhumid study areas in sagebrush steppe of central and eastern Washington state. Symbols denote different transects within each study area. "Excl" refers to long-term, ungrazed exclosure sites.

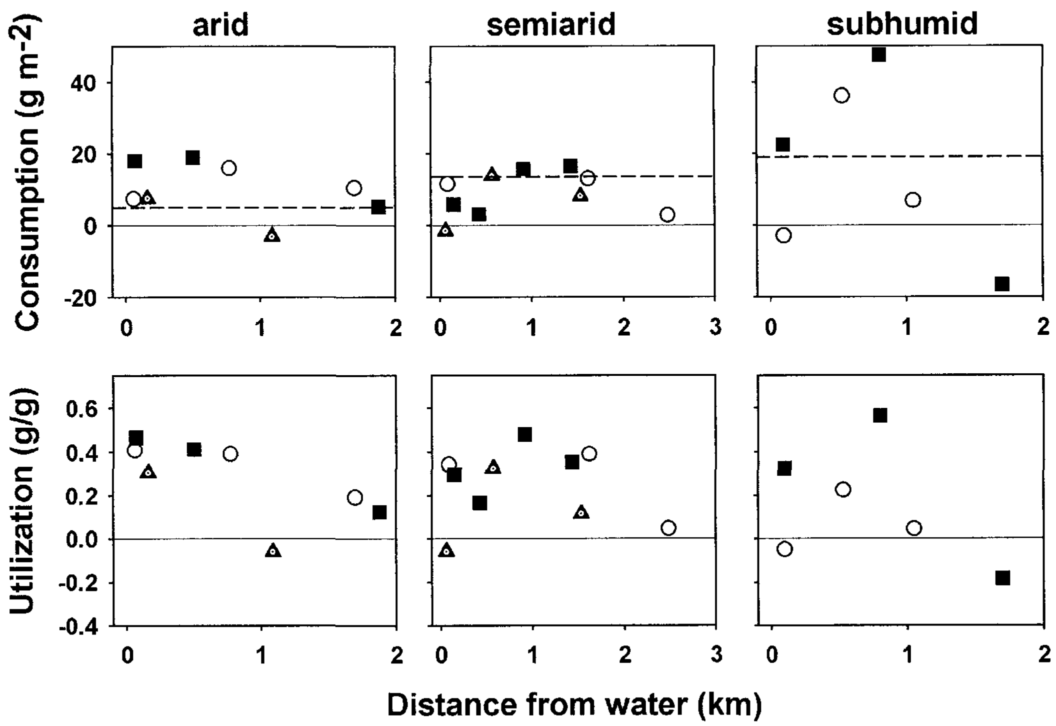

Fig. I.3. Consumption and utilization along distance from water gradients in arid, semiarid, and subhumid sagebrush steppe of central and eastern Washington. Symbols denote different transects within each study area. Points falling below the solid line at consumption and utilization equal to zero occur when biomass in the ungrazed temporary exclosures is higher than biomass in the grazed area due to spatial heterogeneity. The dashed lines in the top panels show expected consumption based on stocking rates and daily forage requirements.

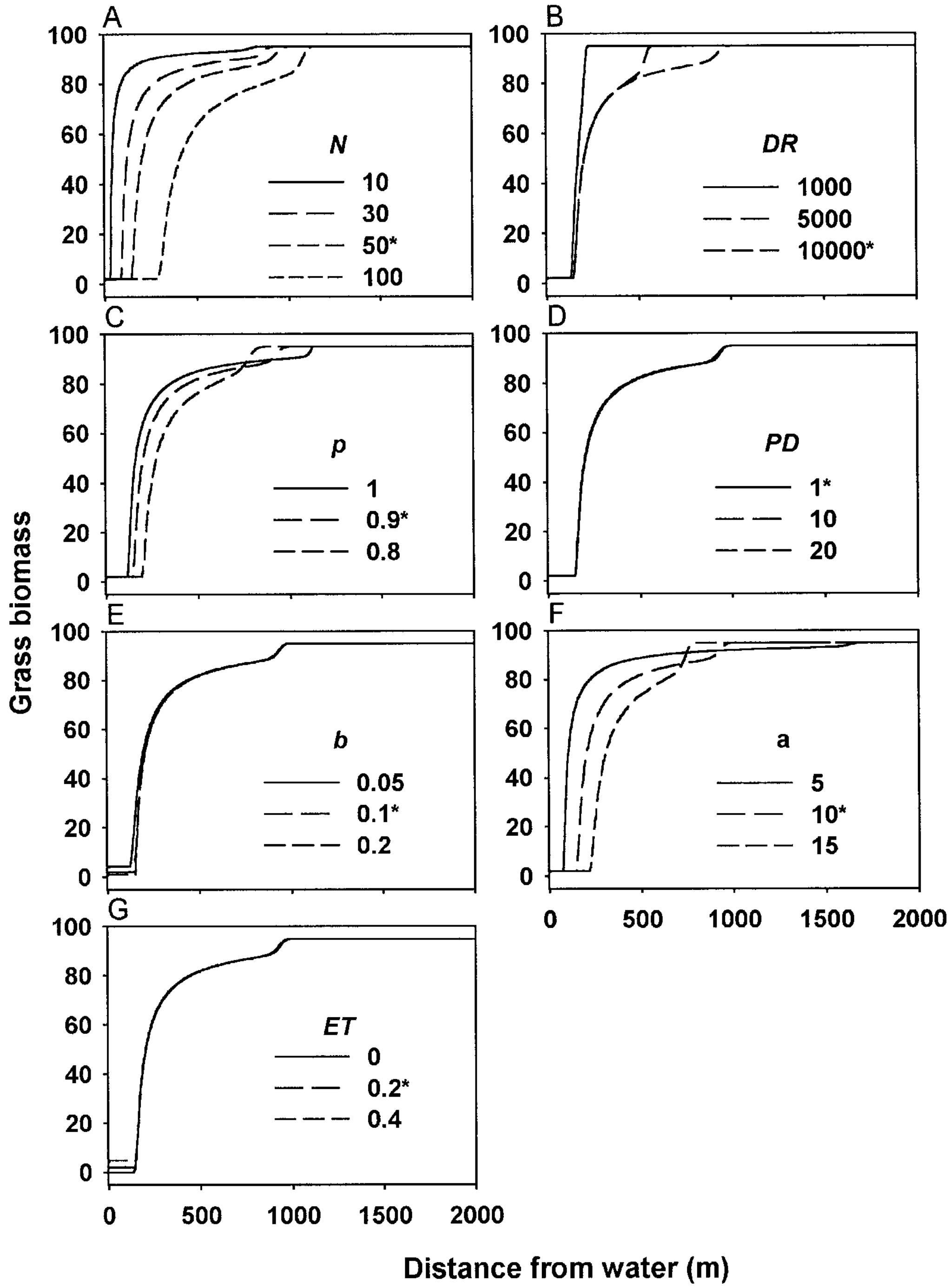

Fig. I.4. The influence of model parameters on simulated grass abundance across a distance from water gradient, using time minimization (TMin) model on a landscape with a point water source. For each simulation, grass biomass is shown at day 300. The *'s indicate parameter values used in simulations comparing different models. Parameters are defined in Table I.1.

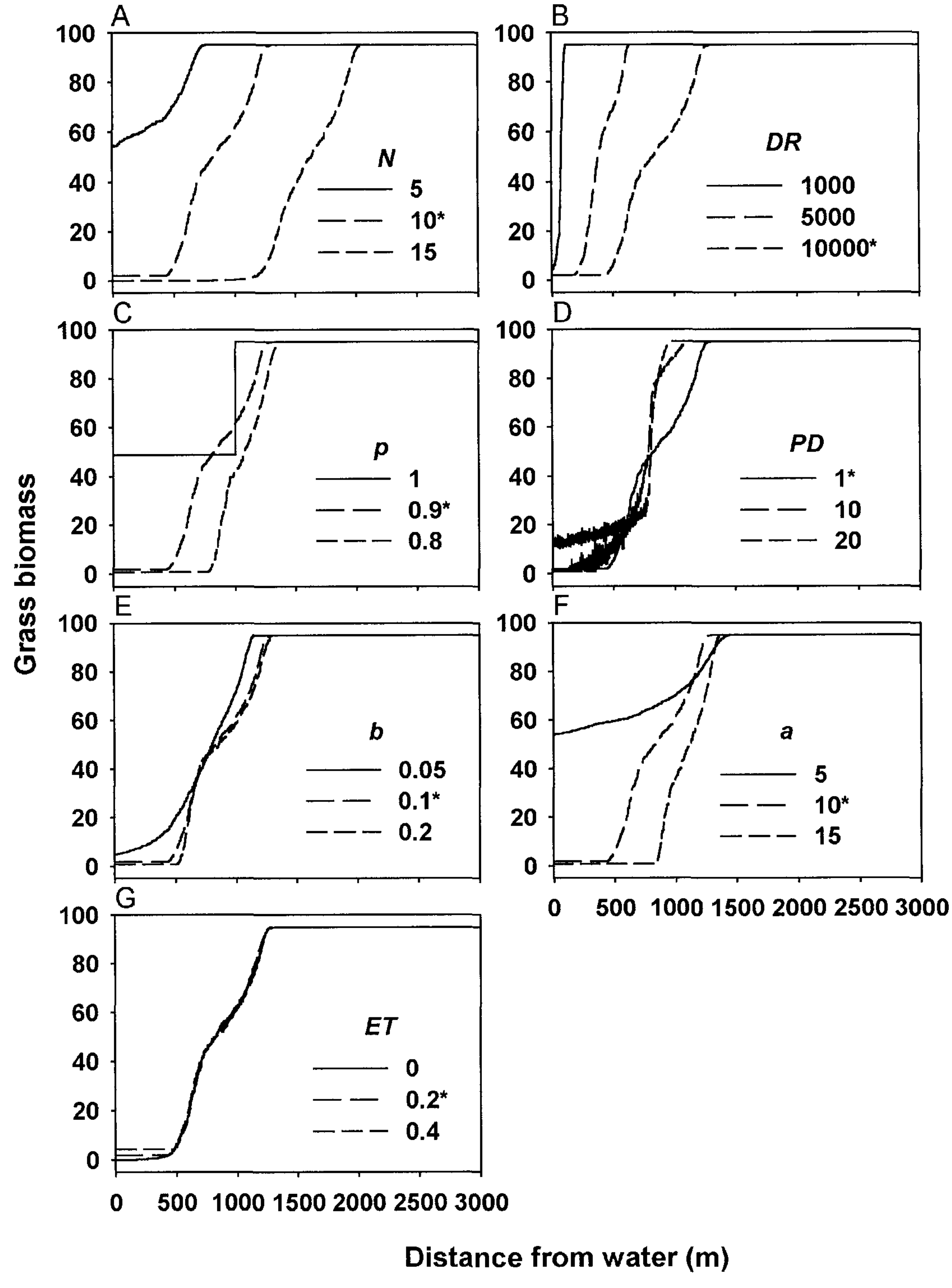

Fig. I.5. The influence of model parameters on simulated grass abundance across a distance from water gradient, using the TMin model on a landscape with a linear water source. For each simulation, grass biomass is shown at day 300. The *'s indicate parameter values used in simulations comparing different models. Parameters are defined in Table I.1.

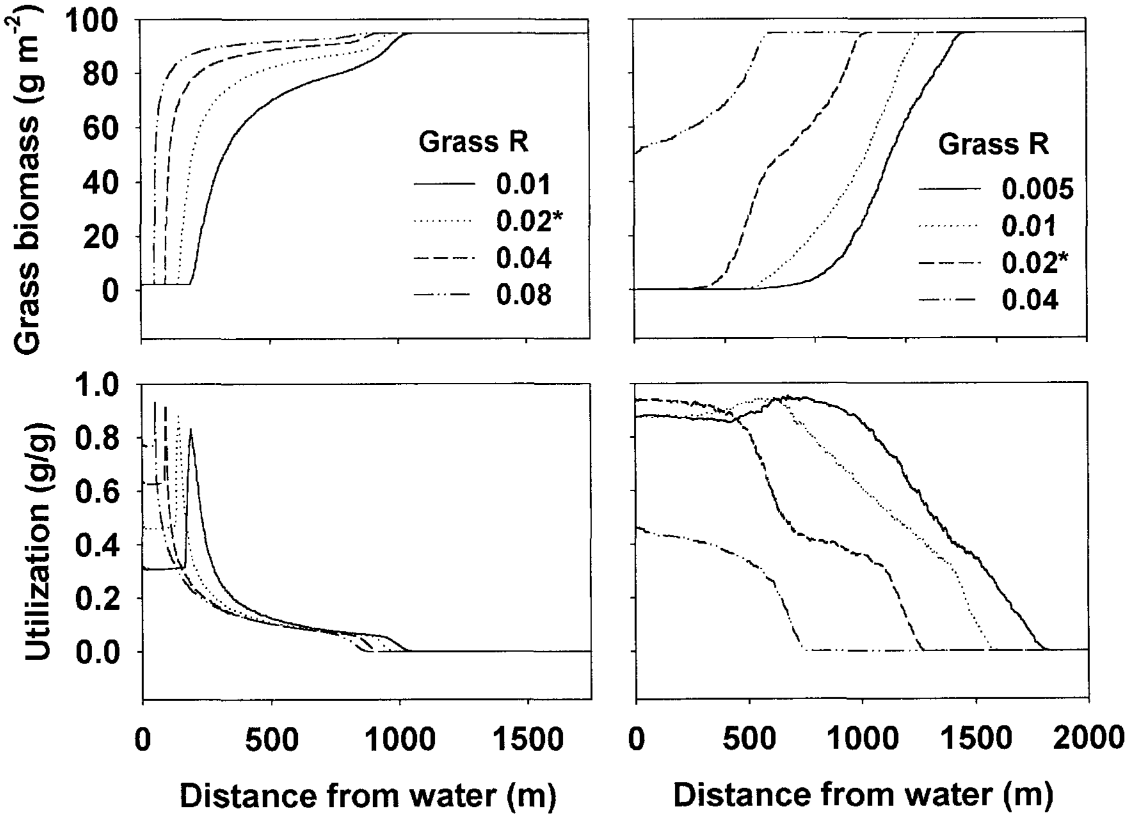

Fig. I.6. The effect of changes in grass instantaneous growth rate (R_G) on patterns in grass biomass and utilization at day 300. Panels on the left show results from the TMin model on a landscape with a point water source, panels on the right show results from a linear water source. The *'s show the value of the parameter used to compare different models.

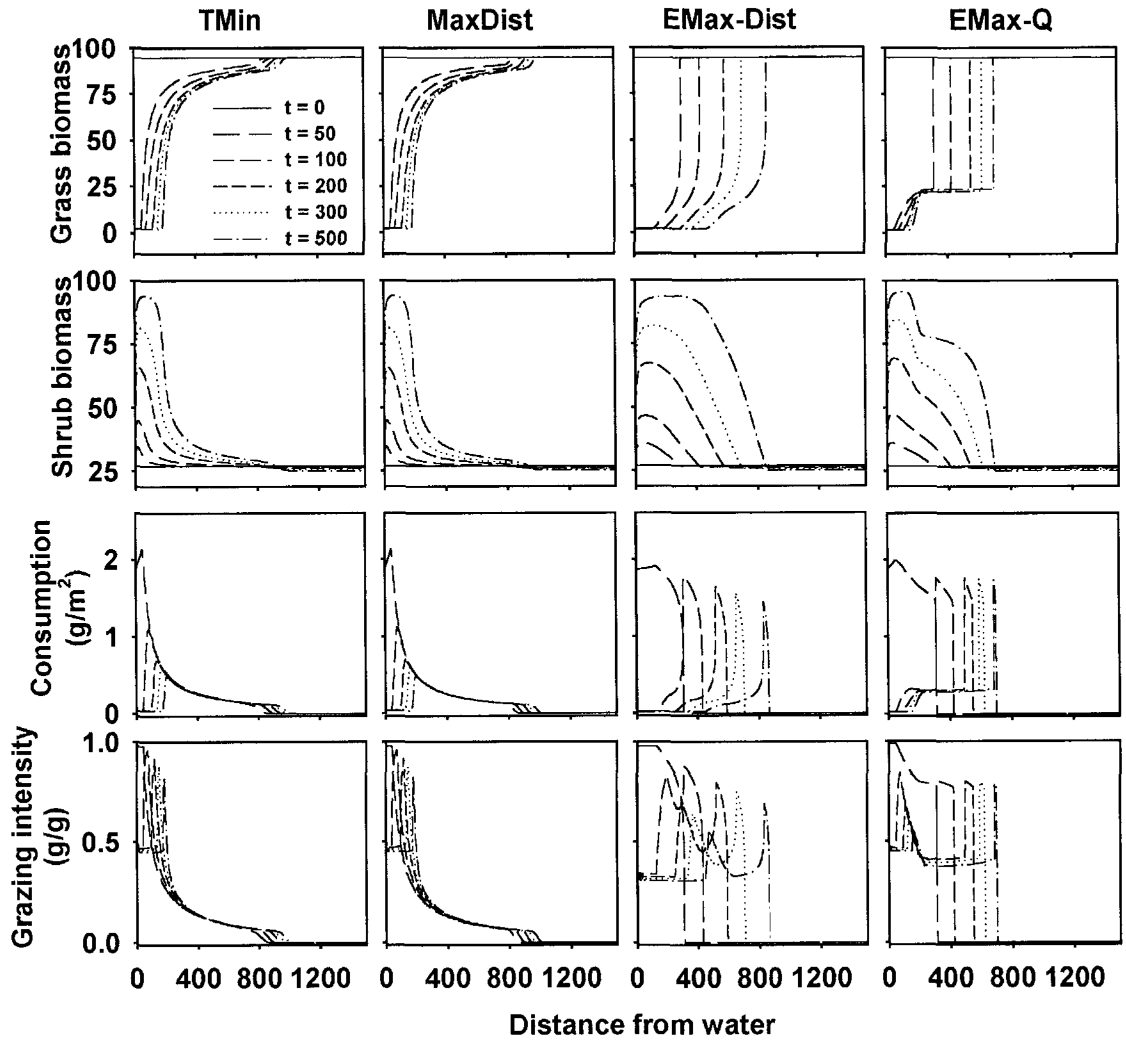

Fig. I.7. Simulated temporal changes in patterns of grass and shrub biomass, consumption, and utilization under different foraging models run on a landscape with a point water source. Lines correspond to patterns at different days (t = 0, 50...500) during the simulation. Consumption and utilization were calculated for the 50 day period preceding each output time.

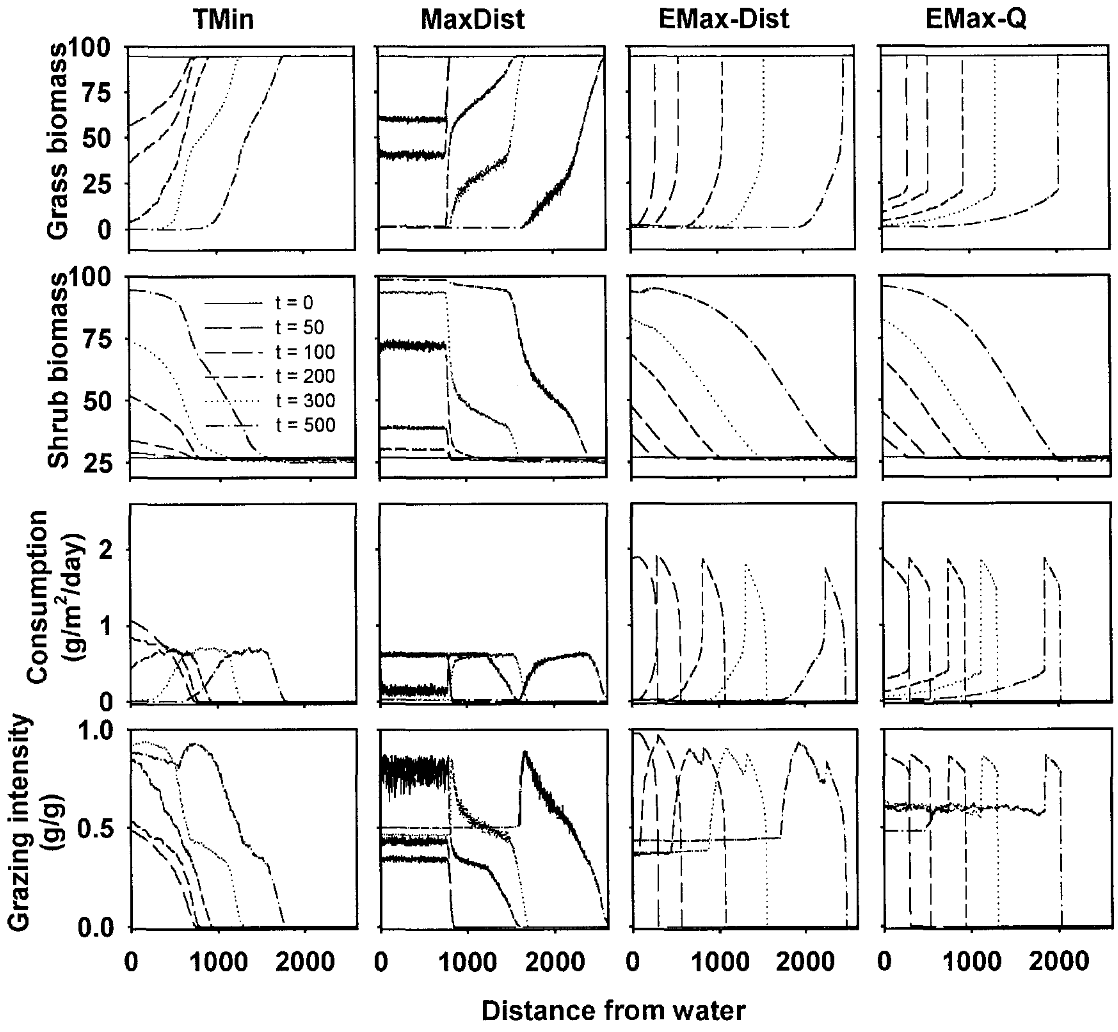

Fig. I.8. Simulated temporal changes in patterns of grass and shrub biomass, consumption, and utilization under different foraging models run on a landscape with a linear water source. Lines correspond to patterns at different days (t = 0, 50…500) during the simulation, however results are reported for the MaxDist model at doubled time intervals (t = 0, 100...1000) because the patterns were much slower to develop. Consumption and utilization were calculated for the 50 day period preceding each output time for all models.

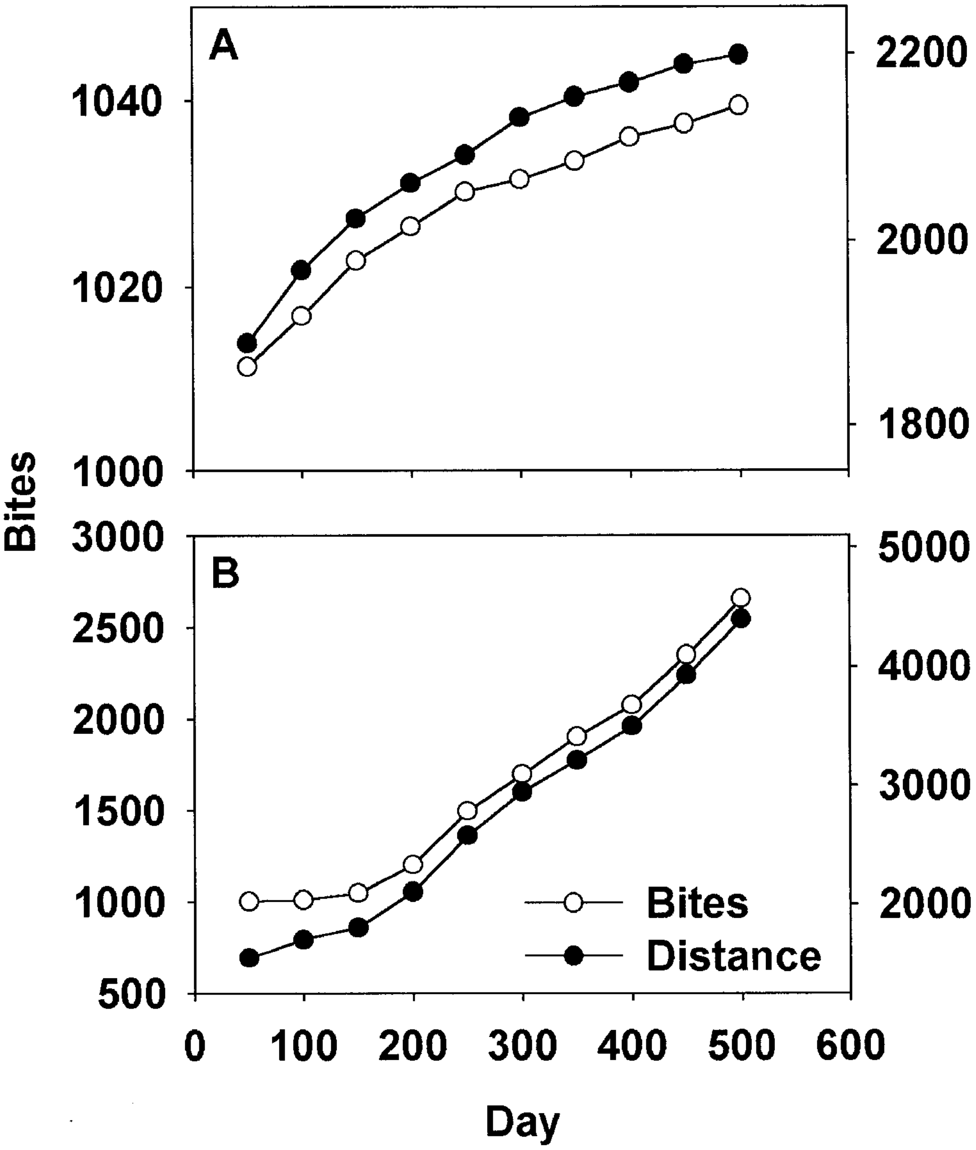

Fig. I.9. Change over time in the mean number of bites taken and distance traveled by grazers. The simulation was run using the TMin model on A) point water source and B) linear water source landscapes.