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Do abiotic differences explain contrasting graminoid functional traits in sagebrush steppe, USA and Patagonian steppe, Argentina?

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Abstract

Previous work in climatically similar sagebrush steppe, USA and Patagonian steppe, Argentina suggested that a more intense evolutionary history of grazing in Patagonia selected for graminoids of lower forage quality, resulting in a plant community more resistant to livestock grazing. Here we consider whether subtle abiotic differences might create greater water or nutrient limitation in Patagonian steppe, which would offer an alternative explanation for the observed contrasts in graminoid functional traits. Simulations of soil water dynamics showed that observed differences in temperatures and wind speeds canceled out, but differences in soil texture were important. The sandier soils typical of Patagonian steppe reduced the ratio of evaporation to transpiration, and may have contributed to a longer growing season in Patagonia, as measured by a satellite index of vegetation activity. Thus, we did not find strong evidence for greater water limitation than in sagebrush steppe, although the larger arid zone within Patagonia might still favor the evolution of xerophytic traits. On the other hand, sandy soils accumulate less total nitrogen than the loamier soils common in

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sagebrush steppe. Older, more weathered soils are also more regionally common in Patagonia. Nitrogen limitation created by coarse textured, weathered soils offers an alternative working hypothesis to explain the evolution of lower forage quality in Patagonian steppe graminoids.

Keywords: Convergence; Evapo-transpiration; NDVI; Soil texture; Sagebrush steppe; Patagonia

1. Introduction

An important goal of research in arid and semi-arid ecosystems is to understand why domestic livestock grazing has dramatic effects on some plant communities, but only subtle effects on others (Milchunas and Lauenroth, 1993). Recent comparative work in the climatically similar sagebrush steppe of North America and Patagonian steppe of South America suggested that the nutritional status of common forage species plays a key role in determining ecosystem impacts of grazing. Common graminoids in Patagonian steppe are much lower in forage quality than sagebrush steppe graminoids (Adler et al., 2004). The lower forage quality in Patagonia leads to lower utilization than in sagebrush steppe and, as a result, smaller changes in species composition and productivity under livestock grazing (Adler et al., 2005).

While differences in functional traits provide a proximate explanation for differences in grazing impacts, to determine the ultimate cause we must ask why poor forage quality evolved in Patagonian but not sagebrush steppe. Two hypotheses are relevant to this issue. First, the convergence hypothesis predicts similar physiological adaptations, ecosystem structure, and function in regions with similar climate (Orians and Solbrig, 1977; Cody and Mooney, 1978; West, 1983). Second, given climatic similarity, differences in each region's evolutionary history of grazing should explain differences in plant traits related to grazing resistance (Mack and Thompson, 1982; Milchunas et al., 1988). The sagebrush–Patagonian steppe comparison fits this logical framework: both systems share strong similarity in climate and ecosystem functioning (Paruelo et al., 1995, 1998) and are dominated by shrubs and caespitose bunchgrass, often from the same genera. But while densities of ungulate grazers in sagebrush steppe have been quite low during much of the Holocene (reviewed by Lyman and Wolverton, 2002), guanaco, a native camelid, occurred in high numbers in Patagonian steppe as recently as the 1970s (Franklin, 1981). This difference in evolutionary history suggests that the poor forage quality of the Patagonian graminoids may have evolved as a defense against grazing by guanaco (e.g. Lauenroth, 1998).

Despite the global scale similarity of these two systems, some abiotic differences are inevitable. Our objective in this paper was to identify abiotic contrasts between sagebrush and Patagonian steppe and evaluate their potential to offer an alternative explanation for the evolution of poor forage quality in Patagonia. We focused on factors that could lead to greater water or nutrient limitation in Patagonia, since low resources select for slower growing plants with long-lived, low quality leaves (Grime, 1977; Chapin, 1980; Cunningham et al., 1999; Wright and Westoby, 1999). First, we used existing data on geological and climatic history and contemporary climate and soils to identify the main abiotic differences between the two regions. We relied heavily on data from long-term field sites, but took advantage of regional spatial data when possible. Second, we assessed the influence of these differences on water availability as measured by a soil water model and a satellite index of vegetation activity, and considered the potential for differences in geology and soils to influence nutrient availability. Our goal was not a definitive test of any one mechanism, but rather a survey of leading candidates to guide future research.

2. Methods

2.1. Study areas

We chose the Arid Lands Ecology Reserve (ALE) on the US Department of Energy's Hanford Reservation in central Washington state (46.6°N, 119.6°W, 560 m a.s.l.), and Río Mayo (RM), a field experiment station administered by the Instituto Nacional de Tecnología Agropecuaria (INTA) in southwestern Chubut province (45.4°S, 70.3°W, 500 m a.s.l.), for a detailed site-to-site comparison. Each of these sites offers long-term daily data for precipitation, wind, and mean and maximum temperature, in addition to data on vegetation (Soriano, 1983; Rickard et al., 1988). Although other field stations in sagebrush steppe offer similar records, only the ALE site has low enough mean annual precipitation to allow a meaningful comparison with RM. Field measurements of above-ground net primary production (ANPP) show that the two sites are well-matched: at ALE, ANPP averaged 72 g m^2 over 4 years (Rickard et al., 1988), while at RM, ANPP of perennial grasses and shrubs averaged 56 g m^2 over 10 years, with little contribution from annuals and forbs (Jobbágy and Sala, 2000).

Because neither one of these individual sites can represent their entire region, we consider broader scale sources of data as well. Both the Intermountain west of North America and southern South America east of the Andes contain a heterogeneous mix of arid and semi-arid ecosystems. For the purposes of comparison, we 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, dominated by perennial bunchgrasses such as *Festuca idahoensis* and *Agropyron spicatum* and the shrub *Artemisia tripartita*, and the bunchgrass-shrub areas correspond to Küchler's "Sagebrush-steppe", dominated by *Agropyron spicatum*, *Stipa* bunchgrasses, and various subspecies of *Artemisia tridentata*. We refer to the combined area of both these vegetation types as sagebrush steppe, and specify grass or shrub-grass areas to identify the specific vegetation type within the region (Fig. 1). The South American study area, located primarily in the southern Argentine provinces of Neuquén, Río Negro, Chubut, Santa Cruz and Tierra del

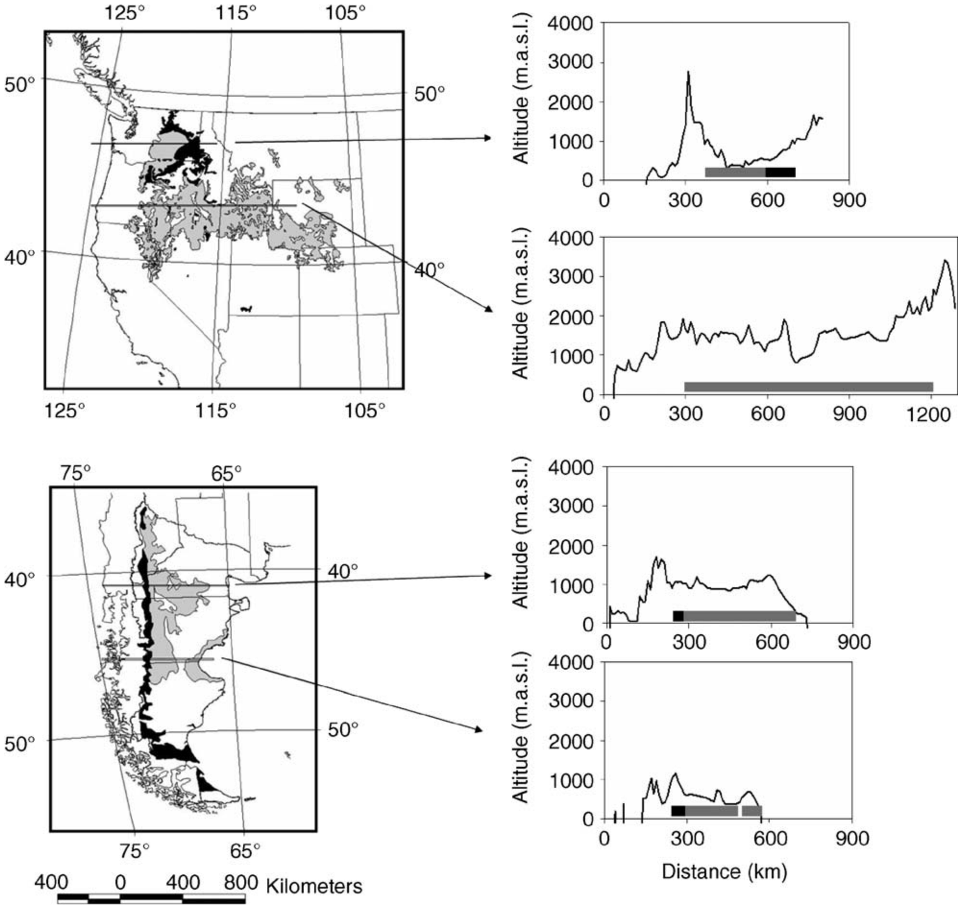

Fig. 1. Bunchgrass (black areas) and bunchgrass-shrub (gray areas) dominated areas of North American and the Patagonian region of South America (based on Küchler, 1964; León et al., 1998). The elevation profiles are based on digital elevation models compiled by the United States Geological Survey (http://edcdaac.usgs.gov/gtopo30/gtopo30.asp).

Fuego, includes the "Subandean District" (Soriano, 1983; León et al., 1998), dominated by the bunchgrass *Festuca pallescens*, and the "Occidental District" and "Gulf of San Jorge District," characterized by *Stipa* bunchgrasses and shrubs including *Mulinum spinosum* and *Senecio filaginoides* (Fig. 1). We refer to these vegetation types collectively as Patagonian steppe. Botanical nomenclature follows Hitchcock and Cronquist (1973) for sagebrush steppe and Correa (1969–1999) for Patagonian steppe. Both ALE and RM are located in grass-shrub areas.

We 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), 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 higher than 40°S.

2.2. Climate data

We compared monthly patterns of precipitation, temperature, and wind speed at ALE (Hoitink et al., 1999) and RM (Beltrán, 1997). Mean monthly wind velocity was available at the 2 m height above the ground for RM and 15 m for ALE. We transformed the ALE data to 2 m based on a standard logarithmic height–wind speed relationship (R. Pielke, pers. comm.), $V_2 = V_{10}\log(H_{\mathrm{RM}}/0.05)/\log(H_{\mathrm{ALE}}/0.05)$, where V_i is velocity at height i and H is the height of observations at each field station. To characterize regional precipitation in the sagebrush steppe, we used mean annual values from Daly et al. (1994). For Patagonia, we combined data from the US National Climatic Data Center (NCDC) and INTA, and then interpolated these data using a distance weighting method (ArcView 3.2). In addition, we show monthly patterns of precipitation and temperature for three additional locations characteristic of different areas within each region (same data sources).

2.3. Soils data

At ALE, we collected five soil cores to 1 m depth then aggregated the cores by 10 cm depth intervals for analysis of texture using the hydrometer method (Gee and Bauder, 1986). We obtained similar data on soil texture at RM from A. Cesa (unpublished data). These soil texture data were used as inputs for the soil water model (described below). For regional data, we used the US 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 we 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).

2.4. Evapo-transpiration

To evaluate the importance of differences between ALE and RM in soil and climate, we estimated evapo-transpiration using the "Soilwat" simulation model (Parton, 1978). We first used the model to estimate evapo-transpiration patterns under mean observed conditions at each site. Then, to evaluate the relative influence of weather and soils on differences in modeled evapo-transpiration, we ran a series of simulations where we substituted input variables from one site to the other. For example, we asked how evapo-transpiration at ALE would change if ALE had RM's soils or experienced RM's winds, and vice versa.

Soilwat requires three classes of input data: (1) vegetation—monthly values for both total and live above-ground biomass, and the proportional distribution of roots in each soil layer; (2) climate—daily precipitation and mean temperature, as well as mean monthly wind speed and radiation, and (3) soils—depths of each soil layer, and for each layer, soil texture and bulk density. Because we were primarily interested in comparing the effects of abiotic differences, we held vegetation constant in all simulations by creating one set of vegetation inputs, averaging monthly biomass values (total and live) from RM (Soriano, 1983) and ALE (Rickard et al., 1988), and taking rooting distributions from RM (Paruelo and Sala, 1995). Peak live biomass increases from winter ($0\,\mathrm{g\,m^{-2}}$) to its peak in early summer ($67\,\mathrm{g\,m^{-2}}$), while total biomass is less variable, and averages about $150\,\mathrm{g\,m^{-2}}$, much of it contributed by shrubs. Since we had 12 complete but not successive years of daily weather data for RM, we matched each RM weather year with an ALE weather year having similar annual precipitation, producing a dataset of 12 independent weather years for each region. We used mean monthly radiation data from ALE for all simulation runs. We based soil layers on the depth zonation of plant roots at RM (Paruelo and Sala, 1995).

In the simulation runs, we held vegetation inputs constant but factorially manipulated ALE and RM values of three input "variables:" (1) daily precipitation and temperature, (2) mean monthly wind speed, and (3) soil texture and bulk density by depth. Each simulation run consisted of 12 independent climate years (fall through summer), with soil water values reset at the start of each climate year. We compared the transpiration, evaporation, change in soil water storage, and transpiration/actual evapo-transpiration (T/AET) averaged across each set of 12 one-year simulations. We chose soil water initialization values so that the mean change in soil water storage, over all 12 years, would be close to zero when running ALE weather and wind on ALE soils, and likewise, RM weather and wind on RM soils. We accomplished this by initializing each soil layer at 80% of the water content at 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.

Because the model is deterministic, we could not use an ANOVA to calculate the error terms for each input variable's effect, or to assign statistical probabilities to these effects. We did, however, calculate the relative main effect of each of the three input variables (precipitation and temperature, wind, and soils) to determine the sensitivity of the model results to these variables. We followed Box et al. (1978) and Paruelo and Sala (1995), calculating the relative main effects as follows. First, we assigned parameter values of $+1$ to ALE inputs and -1 to RM inputs, then multiplied the response variables (mean evaporation, transpiration, and T/AET) by these parameters, and summed each response across all eight-model runs. If, for example, precipitation and temperature have no effect on evaporation, this sum will equal zero. If evaporation is higher under ALE precipitation and temperature, the sum will be positive, whereas a negative sum indicates higher evaporation under RM precipitation and temperature. To allow comparison of different responses, we divided each of these sums by the corresponding mean response across all model runs.

2.5. NDVI

Satellite-derived normalized difference vegetation index (NDVI) provides a measure of radiation interception by vegetation (Box et al., 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. Therefore, we use regional NDVI data to describe the timing and intensity of the growing season (Reed et al., 1994) in each ecosystem.

We used NDVI images provided by NOAA's Advanced Very High Resolution Radiometer (AVHRR). For both sagebrush and Patagonian steppe, we used images from the Pathfinder AVHRR Land program (PAL) with a resolution of 8 km (Agbu and James, 1994; James and Kalluri, 1994), spanning the period from 1981 to 1999 but excluding 1994 due to problems of satellite operation. 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). We reprocessed data from each source to obtain monthly composites for each pixel.

We selected all pixels within the study area in each region (Fig. 1), then filtered out pixels dominated by urban and agricultural land uses in North America 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, we 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). To compare the seasonal NDVI curves for the pixels closest to the ALE and RM study sites, we averaged values by month, across years. To produce the regional curves, we averaged the values of all pixels within each vegetation type (grass and grass-shrub) by month. We did not use results from the three winter months due to inconsistent temporal coverage.

3. Results

3.1. Climate

Since past climates may be as important as contemporary ones in driving plant evolution, we first consider the historical climate of each region. By the mid Pliocene (ca. 3.5 Mya), the Cascade Mountains of Oregon and Washington had reached elevations high enough to create a large rain shadow and summer drought, causing the replacement of mesophytic with xerophytic species (Wolfe, 1969; Daubenmire, 1975). This floristic transition was complete by the Pleistocene, so that the flora during this period was not significantly different from the modern flora. Alternation of cool, wet periods and warmer, drier periods, continued from the Pleistocene through the Holocene, producing range shifts but not large changes in species composition (Daubenmire, 1975; Beiswenger, 1991; Nowak et al., 1994; Jensen et al., 1997; Grayson, 2000). The climate history of Patagonia followed a similar chronology. Andean uplift began in Patagonia in the mid-Miocene and was complete by the end of the Pliocene, creating extensive grasslands and semi-deserts (Solbrig, 1973). 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).

Comparison of contemporary climate data from the ALE field station in sagebrush steppe and the RM field station in Patagonian steppe show similar seasonal patterns of precipitation, with precipitation concentrated in late fall and early winter (Fig. 2A). This seasonality reflects the fact that both regions, at latitudes of roughly 40–50°, are dominated by maritime polar air masses that create cool, moist winters and dry summers. In contrast to the similarity in precipitation, the sagebrush site has greater thermal amplitude than the Patagonian site (Fig. 2B). 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 at the Patagonian site (Fig. 2C). 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 compared to ALE.

Regional climates of the North and South American study areas are characterized by dramatic gradients in precipitation (Fig. 3). 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. By contrast, the Patagonian steppe east of the Andes is quite level, and precipitation declines as a function of distance from the mountains (Jobbágy et al., 1995). While the range of mean annual precipitation is similar in both regions, areas that receive less than 200 mm annually, such as the ALE and RM field stations, cover about 94,000 km^2 of Patagonian steppe, but only 21,000 km^2 of sagebrush steppe (study areas shown in Fig. 1). This comparison would be even more lopsided if we considered the extremely arid, shrub-dominated areas of central Patagonia (arid, shrub dominated areas of North America generally occur in the hot deserts to the south of sagebrush steppe, not interspersed with grass steppes as in Patagonia). Thus, while the RM site is representative of large areas of Patagonian steppe, ALE is warmer and drier than most sagebrush steppe, in large part due to its low elevation (Fig. 1).

The greater thermal amplitude at ALE compared to RM also can be seen at the regional level: sites across the sagebrush steppe have hotter summers and cooler winters than Patagonian sites (Fig. 3). This potentially important difference is obscured by simple comparisons of mean annual temperature.

The two-fold difference in wind speed characterizes the broader regional comparison as well, and in fact Patagonia has some of the highest average wind

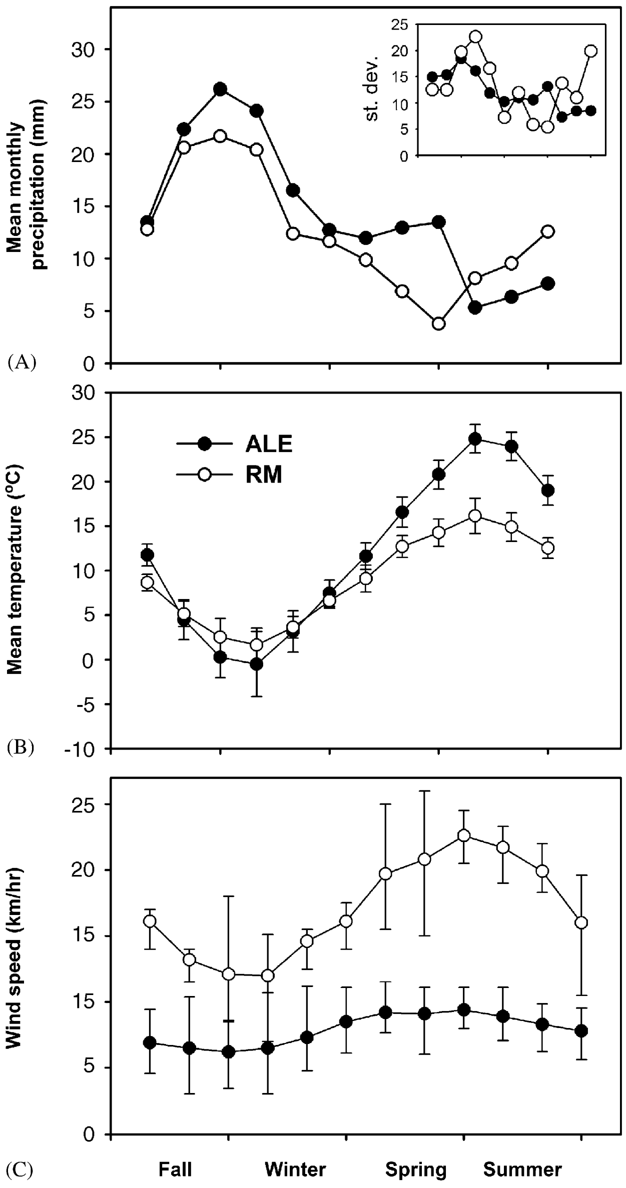

Fig. 2. Comparison of climate at the Arid Lands Ecology reserve (ALE) in the sagebrush steppe, and the Río Mayo Experimental Station (RM) in Patagonian steppe. (A) Mean monthly precipitation, with the inset showing standard deviation (among years). (B) Mean monthly temperature, with error bars showing ±1 standard deviation. (C) Mean monthly wind speed, with error bars showing mean maximum and mean minimum monthly wind speeds. The order of months shown is October–September for ALE, and April–March for RM. Data are from Hoitink et al. (1999) for ALE and Beltrán (1997) for RM.

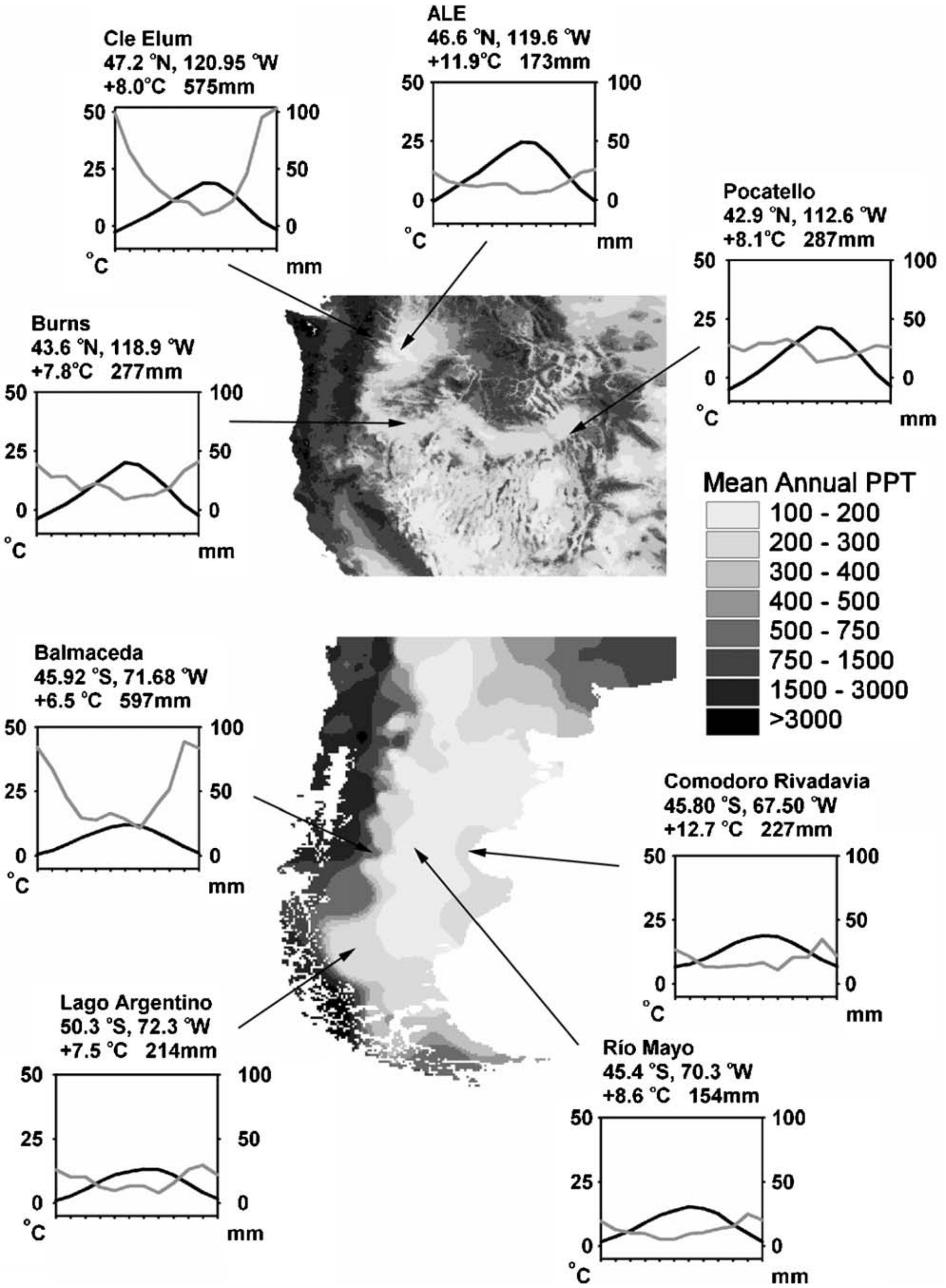

Fig. 3. Mean annual precipitation maps for the sagebrush and Patagonian steppes, and detailed climatic information for selected locations. The sagebrush steppe precipitation map is based on Daly et al. (1994), and the Patagonia map is an interpolation based on over 60 weather stations. The horizontal axes of the climate diagrams show months January–December for sagebrush steppe and July–June for Patagonia. Note that the two regions are not mapped at the same scale.

speeds of any terrestrial area (NASA's Earth Science Enterprise Program provides online visualizations at http://eosweb.larc.nasa.gov/sse/).

3.2. Geology and soils

Since the parent materials of contemporary soils are determined by geological processes, we briefly review the geology of each region. 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 (Solbrig, 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.

Soils at the ALE field station are silty loams derived from wind-deposited loess (40% sand) with a calcareous horizon below 90 cm (Rickard et al., 1988). Soils at the RM field station in Patagonia are loamy sands and sands (85–90% sands) derived from fluvial deposits with a calcareous layer at approximately 60 cm depth (Paruelo and Sala, 1995). These differences reflect broader regional contrasts revealed by comparing the distribution of soil types in each region. 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. 4). In Patagonia, 78% of soils are ‘‘sandy,’’ compared to only 29% in the sagebrush steppe.

A second 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 1). This difference reflects the greater area of extremely arid climate within Patagonia. Finally, older, well-developed soils are more abundant in Patagonia (Haplargids, Paleorthids). 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.

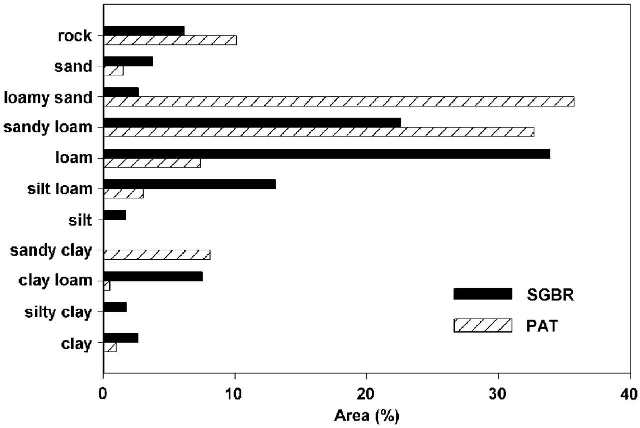

Fig. 4. Soil texture by area in sagebrush (SGBR) and Patagonian (PAT) steppe. Analysis is based only on areas dominated by grasses or grasses and shrubs (see Fig. 1).

Table 1
Common soils of the sagebrush steppe, North America, and Patagonian steppe, South America

Great Group	Sagebrush steppe (%)	Patagonian steppe (%)
Torriorthents	10.8	17.0
Cryoborolls	11.2	0.7
Paleorthids	0.3	10.7
Haplargids	8.8	10.3
Rock	2.9	10.1
Argixerolls	8.9	4.0
Haploborolls	1.4	7.9
Natrargids	1.3	7.5
Vitrandepts	0.1	5.7
Haploxerolls	5.5	3.9
Xerorthents	0.5	5.0
Argiborolls	3.9	0
Paleoargids	0.4	3.7
Cryochrepts	3.8	0
Camborthids	3.5	2.1
Calciorthids	3.0	2.4
Torripsamments	2.9	1.6
Cryoboralfs	2.8	0
Xerochrepts	2.3	0
Ustorthents	2.3	0
Durargids	2.1	0
Total shown	78.7	92.6

Shown are Great Groups covering at least 2% of the total area of one of the two regions.

3.3. Evapo-transpiration

The 12 weather years from ALE and RM used as model inputs are well matched in terms of annual precipitation and are representative of long-term precipitation seasonality at each site, with 25–30% of precipitation falling during autumn, over 35% in winter, about 20% in spring, and under 15% in summer.

At ALE, simulated evaporation was slightly higher, and transpiration lower, than at RM, resulting in a 2% difference in the efficiency of rain use, defined as transpiration divided by actual evapo-transpiration (T/AET) (Table 2). To determine which factor caused this difference, we ran a series of simulations substituting input variables from one site to the other. Simulations using 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). 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 more efficient use of precipitation (T/AET) no matter which weather inputs were used (Table 2). The relative main effects showed that the increases in evaporation and decreases in transpiration and T/AET caused by ALE precipitation and temperature relative to RM precipitation and temperature were opposite in direction and of slightly lower magnitude compared to the effects of differences in wind (Fig. 5). Differences in soil had larger effects than either wind or precipitation and temperature, with evaporation higher on ALE soils, but transpiration and T/AET higher on RM soils.

Regardless of model inputs, inter-annual variability was high. For example, running the model with ALE weather and soils, mean transpiration among years was 49.8 mm, but the 95% confidence intervals ranged from 37.1 to 62.6 mm. For RM

Table 2
Results from the soil water model simulations

Ppt & Temp	Wind	Evap.	Transp.	AET	ΔSoil water (mm)	T/AET
On 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
On 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

Shown are means (mm) from 12 independent one-year runs, using different combinations of observed ALE or RM inputs for daily temperature and precipitation (Ppt & Temp), monthly wind speed, and soils. "ΔSoil water (mm)" is the difference between the first and last day of each year in soil water stored in the whole soil profile.

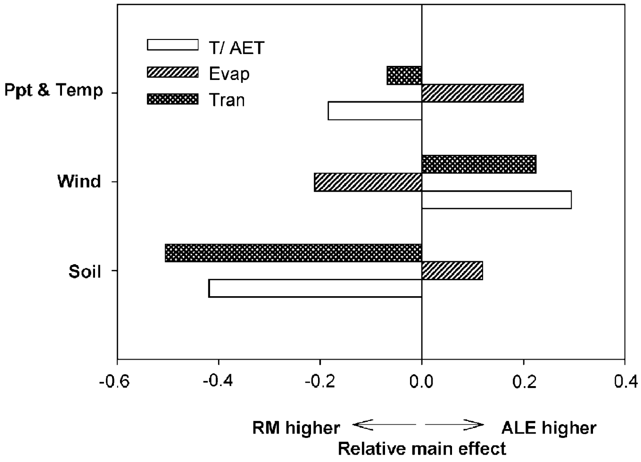

Fig. 5. Relative main effects of differences in ALE and RM precipitation and temperature (Ppt & Temp), wind, and soil on simulated evaporation (Evap), transpiration (Tran), and transpiration/actual evapotranspiration (T/AET). Positive values indicate higher responses under ALE inputs, while negative values indicate higher responses under RM inputs. Main effects were normalized by dividing by the corresponding mean to allow comparison among response variables. The main result is that differences in soils were more important than differences in weather in explaining simulated contrasts between ALE and RM.

weather and soils, transpiration averaged 54.8 mm, with a 95% confidence interval from 43.1 to 66.4 mm. Evaporation was similarly variable.

The mean seasonality of simulated 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. 6). Using RM climate (temperature, precipitation, and wind), transpiration was marginally higher during late summer and fall, and marginally lower during early summer, compared to simulations using ALE climate (Fig. 6).

3.4. NDVI

Mean monthly NDVI in the 8 × 8 km individual pixels corresponding to ALE and RM, locations with similar rainfall, were remarkably similar, with values of 0.189 and 0.183, respectively. However, seasonality of NDVI clearly differed: at ALE, NDVI had a narrow peak in late spring, whereas at RM, NDVI was relatively uniform from spring through fall, with some indication of a bimodal distribution (Fig. 7 inset).

At the regional scale, NDVI for grass dominated and grass-shrub co-dominated areas was higher in sagebrush compared to Patagonian steppe (Fig. 7). Mean NDVI, spring through fall, was 0.350 and 0.216 in sagebrush grass and shrub-grass areas, respectively, and 0.236 and 0.179 in Patagonian grass and shrub-grass areas. However, spatial variability was high, with coefficients of variation of monthly

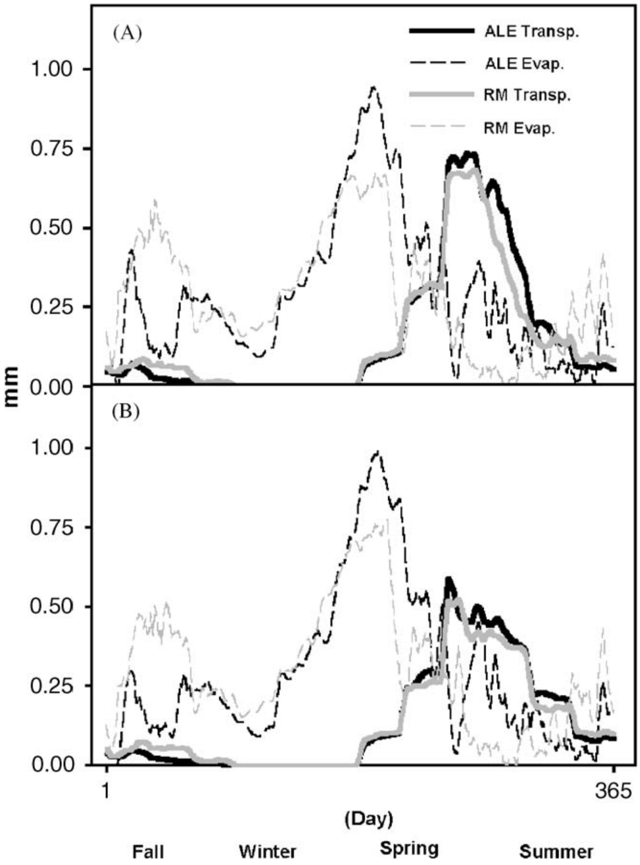

Fig. 6. Results from the soil water model analysis. Panel (A) shows means from runs using RM (Patagonian site) soil parameters, and (B) shows means from runs using ALE (sagebrush site) soil parameters. The lines are 5-day running averages of modeled mean ($n = 12$) daily transpiration and evaporation using ALE weather and wind or RM weather and wind. Day 1 corresponds to September 1 in ALE and March 1 in RM.

means (averaging across pixels) ranging from 28% in sagebrush grass areas to 39% in Patagonian grass areas, meaning that differences in NDVI among vegetation types represent crude trends. Furthermore, comparisons of mean NDVI for large vegetation types may be confounded by differences in the way the vegetation types are defined in each region.

Comparisons of seasonality should be less sensitive to differences in the mapping of vegetation types. Peak NDVI occurred during the month of the summer solstice for all areas except the Patagonian shrub-grass region, which peaked one month earlier. Seasonal NDVI dynamics in both sagebrush steppe vegetation types featured a steep climb to a well-defined peak, followed by a rapid decline (Fig. 7). In Patagonia, the lack of a well-defined peak in NDVI suggests a longer growing season than in sagebrush steppe. Comparing NDVI seasonality at the ALE site to the

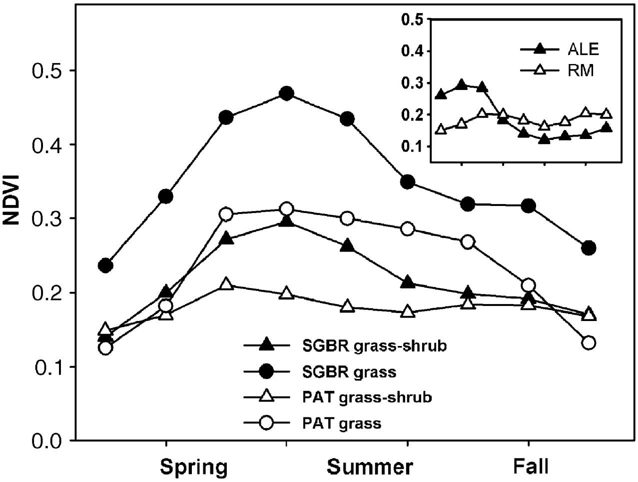

Fig. 7. Satellite-derived mean monthly NDVI for grass and grass-shrub vegetation types in sagebrush and Patagonian steppe (map shown in Fig. 1). The inset shows mean monthly NDVI for one 8 × 8 km pixel located on ALE, in sagebrush steppe, and RM, in Patagonian steppe. The three winter months in each region were excluded because of inconsistent coverage.

broader region shows the relatively earlier phenology at ALE, due to its low elevation and warm temperatures. In contrast, RM is quite representative of seasonality across the Patagonian steppe.

4. Discussion

We found strong similarity in the quantity and seasonality of precipitation in both regions, dating back to the Pliocene, but potentially important differences in the spatial extent of extremely arid zones, thermal amplitude, mean wind speed, and soil texture. We now consider whether these differences could lead to greater water or nutrient limitation in Patagonian steppe, which might explain the lower quality of the Patagonian graminoids.

4.1. *Water availability*

We evaluated the relative importance of differences between ALE and RM in temperature, wind, and soils using a soil water model. The model results were consistent with previous work at RM, including a simulated ratio of transpiration to evaporation of 0.34, identical to the result of an independent model constructed for RM vegetation (Paruelo and Sala, 1995). The model showed that the regional differences in climate and soils did not translate into large differences in evapotranspiration dynamics: running the model with constant vegetation under either ALE climate and soils or RM climate and soils led to a mean simulated difference in transpiration of only 9%, but the 95% confidence intervals were largely overlapping. More detailed model runs, in which we varied climate variables one at a time, explain this similarity. Sagebrush steppe experiences hotter summers than Patagonian steppe, increasing evaporation. But the Patagonian steppe experiences much stronger winds, which also increase evaporation, offsetting the effect of the temperature difference. The single abiotic variable with the strongest effect on evapotranspiration was soil texture. The sandy Patagonian soils allowed higher precipitation use efficiency, presumably because infiltration is faster on coarse soils, allowing water to reach deeper soil layers and escape evaporation. Overall, the soil water model showed that, given similarity precipitation, differences in temperature, wind, and soils do not create greater water limitation in Patagonian steppe, and may even decrease water stress relative to sagebrush steppe.

Although this comparison of two sites with similar precipitation did not produce evidence for greater water stress in Patagonia, differences in the regional spatial distribution of precipitation could have implications for plant evolution. While steep 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. Thus, ALE represents just the most arid portion of the sagebrush steppe, while precipitation at RM is characteristic of broad areas of Patagonian steppe. Isolation offered by the larger 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, by contrast, the small, fragmented areas receiving less than 200 mm of rainfall might have received too much gene flow from surrounding, more productive areas to permit evolution of extremely xerophytic varieties.

Since the soil water model uses growing season length as an input variable, we 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 a longer period of vegetation activity in Patagonian steppe, compared to a short but intense period of activity in sagebrush steppe. The longer growing seasons observed in Patagonia is 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.

Comparison of ALE and RM revealed striking similarity in mean NDVI. At the regional scale, however, we found higher NDVI values in sagebrush compared to Patagonian steppe. This difference may be an artifact of the different ways that grass and shrub-grass vegetation types were defined in each region. The Patagonian shrub-grass type contains larger areas of true aridity than the analogous sagebrush type, explaining why its mean NDVI is lower. The Patagonian grass type may also be drier, on average, than the sagebrush grass zone we delineated. Other potential causes for the observed differences could include degree of ecosystem degradation, cover of biological soil crusts, or influences of surface texture and mineralogy on reflectance (e.g. Asner et al., 2003).

How the invasion of vast areas of sagebrush steppe by the Eurasian annual grass *Bromus tectorum* (Mack, 1981) might confound the regional comparison of NDVI is uncertain. Although the accelerated phenology and lower leaf area of *B. tectorum* compared to native bunchgrasses are clearly demonstrated by field measurements, these differences appear only weakly in remotely sensed vegetation indices such as NDVI. Differences in the NDVI signature of the native vegetation and *B. tectorum* are statistically significant but subtle (Kremer and Running, 1993; Bradford, 2004), probably due to noise created by the spectral signatures of standing dead biomass and, more importantly, the extensive bare soil in these arid and semi-arid environments.

4.2. Nutrient availability

The soil differences we identified may influence nutrient availability, in addition to their effects on seasonality. We did find some evidence of older, more weathered soils in Patagonia, which might suggest nutrient limitation. But given the similarity in soil parent material and age it is unlikely that this difference in weathering would have strong implications for plant nutritional status. The coarser soils of Patagonia, reflecting a history of alluvial rather than aeolian deposition (West, 1983), are a more likely cause of nitrogen limitation. Sandy soils have higher nitrogen mineralization rates and accumulate less total nitrogen than finer textured soils (Schimel et al., 1985a, b; Barrett and Burke, 2002) that may stabilize more N through adsorption and aggregation onto clays (Schimel et al., 1985a). In fact, total soil N was much lower on the sandy soils of arid Patagonia than loamier soils in sagebrush steppe sites with similar above-ground primary production; in more humid sites in each region, where the difference in soil texture was smaller, the different in soil total N was smaller as well (Adler et al., 2005). Lower total N and higher N losses on sandy soils could lead to nitrogen limitation, in turn explaining the lower N content of the Patagonian graminoids (Adler et al., 2004).

Growing season length could interact with N limitation to further influence plant tissue quality. The NDVI data suggest that sagebrush steppe growing seasons are short but intense, whereas growing seasons in Patagonia last longer, but have lower peaks. The shorter growing season of the sagebrush steppe might require fast growth and high N leaves, whereas Patagonia's longer growing season might favor plants with longer-lived, slower growing leaves lower in N (Wright and Westoby, 1999; Wright et al., 2004).

5. Conclusions

One explanation for the evolution of poorer forage quality in Patagonian compared to sagebrush steppe involves a more intense evolutionary history of grazing in Patagonia. Our analysis of abiotic differences indicates that nitrogen limitation caused by the coarse soils of Patagonia offers the most credible alternative hypothesis. We found less evidence for important differences in water stress, though it is possible that the larger arid regions within Patagonia favored the evolution of xerophytic traits. The N limitation hypothesis could be tested by sampling soil and plant tissue N across gradients of soil texture, holding precipitation constant. Rather than acting independently, evolutionary history of grazing and N limitation are likely to interact to influence plant traits. Since losses of leaf-tissue to herbivores are particularly difficult to replace when N is limiting (Coley et al., 1985), selection for plant defense against historical grazing may have been much stronger in Patagonian than sagebrush steppe.

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