

# Functional traits of graminoids in semi-arid steppes: a test of grazing histories

PETER B. ADLER\*, DANIEL G. MILCHUNAS†, WILLIAM K.  
LAUENROTH\*†, OSVALDO E. SALA‡ and INGRID C. BURKE\*†

\*Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523, USA; †Department of Forest, Rangeland and Watershed Stewardship, Colorado State University, Fort Collins, CO 80523, USA; and ‡Department de Ecología, Facultad de Agronomía, Universidad de Buenos Aires, Avenue. San Martín 4453, Buenos Aires C1417DSE, Argentina

## Summary

1. Understanding variability in ecosystem response to grazing is essential for improving management. Recent efforts have focused on the role of plant functional traits but do not identify factors influencing trait development. As traits are legacies of historical selective pressures, they may indicate the importance of a plant community's evolutionary history of grazing.
2. We compared grazing-resistance traits of graminoids collected in the Patagonian steppe of Argentina, presumed to have a long evolutionary history of grazing, and the sagebrush steppe of the north-western USA, known to have a short grazing history. The purpose of this comparison was to test the influence of grazing history and aridity on resistance traits, and to generate predictions about the vulnerability of these ecosystems to grazing impacts. We measured both morphology and leaf chemical composition on common species from an arid and a semi-arid site in each region, then performed a principal components analysis on the species-by-traits matrix.
3. The first axis of the ordination was correlated with measures of forage quality such as leaf tensile strength, fibre and nitrogen content, while the second axis was correlated with plant stature. The dominant species from the drier Patagonia site scored significantly lower on the first axis (lower forage quality) than dominants from the sagebrush steppe. Plants from the wetter Patagonia site were intermediate in forage quality. Sagebrush steppe species scored significantly higher on the second axis (taller) but this difference was not significant when we considered only dominant species.
4. The intercontinental differences in plant traits are consistent with evidence indicating a longer evolutionary history of grazing in Patagonia. Differences in traits between the dry and wet sites in Patagonia are consistent with the hypothesis that aridity promotes grazing resistance, although trait contrasts between the drier and wetter sagebrush sites were not significant.
5. Differences in soil texture, which may influence nitrogen availability, offer an alternative explanation for differences in forage quality between Patagonia and sagebrush steppe, and between the drier and wetter sites within Patagonia.
6. *Synthesis and applications.* Our comparison of plant traits suggests that interactions between evolutionary history of grazing and abiotic covariates, especially soil texture, have selected for low forage quality in Patagonia relative to sagebrush steppe. This contrast in grazing-resistance traits leads to the prediction that livestock grazing will have less impact on upland plant communities in Patagonian steppe compared with the sagebrush steppe of the USA, particularly if low nitrogen content limits offtake. Plant functional traits represent an easily quantified link between evolutionary grazing history and ecosystem responses to contemporary management.

*Key-words:* avoidance, defence, herbivory, Patagonia, sagebrush steppe, tolerance

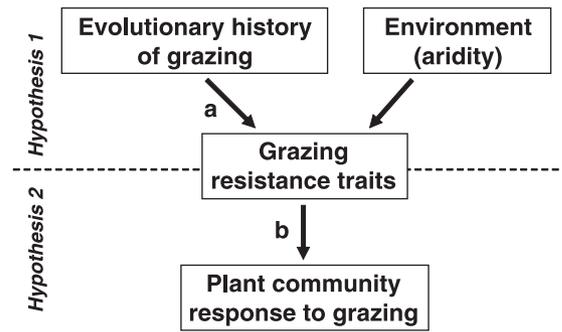
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## Introduction

Recent attempts to explain the great variability in ecosystem response to grazing (Milchunas & Lauenroth 1993) have focused on the role of plant functional traits. The general hypothesis states that the sensitivity of plant communities to grazing depends on the frequency and strength of adaptations helping plants avoid or tolerate herbivory (van der Meijden, Wijn & Verkaar 1988; Díaz, Acosta & Cabido 1992; Lavorel, McIntyre & Grigulis 1999; McIntyre *et al.* 1999; Díaz, Noy-Meir & Cabido 2001; McIntyre & Lavorel 2001; Vesik & Westoby 2001). This hypothesis predicts that grazing impacts will be smaller in systems where grazing-resistance traits 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 & Lauenroth 1993; Díaz, Noy-Meir & Cabido 2001; McIntyre & Lavorel 2001; Westoby *et al.* 2002), cross-system generalizations appear elusive (Vesik & Westoby 2001; Vesik, Leishman & Westoby 2004).

Even if research on plant traits advances to allow predictions of grazing response, understanding differences among ecosystems also requires identifying the origins of differences in plant traits. Two factors are particularly important in determining grazing-resistance traits: aridity and the evolutionary history of grazing (Milchunas, Sala & Lauenroth 1988). 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 defence, these traits can be viewed as 'exaptations' rather than adaptations (Gould & Lewontin 1979). The evolutionary history of grazing (Larson 1940; Stebbins 1981; Mack & Thompson 1982; Milchunas, Sala & Lauenroth 1988) refers to the history of selective pressure on plants exerted by populations of generalist herbivores. Grazing-resistance traits that evolve in response to these selective pressures are true adaptations to grazing.

The evolutionary history of grazing concept has influenced grazing research for more than two decades (Mack & Thompson 1982; Milchunas, Sala & Lauenroth 1988), yet it remains a thinking tool more than a quantitative predictor. Testing predictions based on a system's evolutionary history is problematic because quantifying evolutionary history is difficult. Milchunas & Lauenroth (1993) relied on subjective estimates of the length of the evolutionary history of grazing to test predictions about ecosystem response. Such estimates require information on historical populations of native herbivores over some relevant time period, typically assumed to be in the order of millennia (but see Burkhardt 1996). Another assumption of this approach is that plant species ranges have remained constant over the period of interest, since recent immigrants from other regions could have experienced different grazing histories.



**Fig. 1.** Restatement of the Milchunas, Sala & Lauenroth (1988) model, making explicit the role of plant traits involved in grazing resistance (avoidance and tolerance). We used information on plant traits to make inferences about evolutionary history of grazing, moving in reverse on the arrow labelled 'a', and also to generate predictions about plant community responses to grazing, as indicated by arrow 'b'.

We can circumvent these problems by restating the Milchunas, Sala & Lauenroth (1988) 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 specify two separate hypotheses. First, the main controls on the development of grazing-resistance traits are the evolutionary history of grazing and environmental factors related to aridity. Secondly, because grazing-resistance traits mediate plant-herbivore interactions, such traits are the direct determinants of ecosystem response to grazing (Fig. 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.

Rigorous tests of predictions generated by the second hypothesis are possible because we can easily measure many plant traits. However, evaluating the first hypothesis will remain a challenge because of difficulties in quantifying evolutionary history and unravelling 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, as functional traits are the legacy of historical selective pressures, their frequency and strength will provide evidence for an ecosystem's evolutionary history of grazing. 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, we compared functional 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 influence of aridity on plant adaptations to grazing, climate can confound trait comparisons. The 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 functioning (Paruelo *et al.* 1998). Furthermore, strong precipitation gradients in both regions allow testing of the hypothesis that aridity influences trait development.

Secondly, domestic livestock grazing is an important land use and evolutionary grazing history is a debated topic in these regions. While Milchunas, Sala & Lauenroth (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 (Díaz, Acosta & Cabido 1994; Díaz, Noy-Meir & Cabido 2001) noted apparent adaptations to grazing in the vegetation, suggesting a more intense history of grazing. The importance of guanaco *Lama guanicoe* (Müller), a native camelid, to the indigenous peoples of Patagonia and the number of guanaco hides harvested by modern hunters, support this view (Franklin 1981). In contrast, there is strong consensus that ungulate numbers on the sagebrush steppe were very low during the 2000 years preceding European settlement, probably due to a combination of low productivity, dispersal barriers and hunting by humans (van Vuren 1987; Lyman & Wolverton 2002). If, in fact, grazing has been a more important selective pressure in the Patagonian steppe than in the sagebrush steppe, graminoids from Patagonia should have superior grazing resistance.

In this study, we compared morphological traits and general leaf tissue chemistry of common graminoids from 'dry' and 'wet' semi-arid sites in both sagebrush and Patagonian steppe. The traits we measured were primarily avoidance traits: they limit the amount of biomass plants lose to grazers. Grazing tolerance, the ability of plants to grow and reproduce following defoliation, is often described as an alternative strategy to grazing avoidance (Strauss & Agrawal 1999; de Jong & van der Meijden 2000). However, tolerance is difficult to quantify and, when measured in glasshouse defoliation experiments (Bock, Jolls & Lewis 1995; Adler 2003), common garden experiments (Anderson & Briske 1995) and natural communities (Hendon & Briske 2002) can be a poor predictor of plant population responses to grazing in the field. Nevertheless, some of the avoidance traits we used are correlated with tolerance, such as nitrogen concentration, which influences both palatability and growth rate (Westoby *et al.* 2002). Therefore, we refer to the set of traits we sampled under the umbrella term 'grazing-resistance traits'. Our comparison was further limited to graminoid species, which have few chemical defences relative to herbaceous dicotyledon and woody plants (Coughenour 1985; Vicari & Bazely 1993; but see Redak 1987), relieving us of the need to screen for multiple secondary compounds. Focusing the comparison to one functional group may also help limit the spread of trait values within a site, which often can be as large as the spread between sites (Westoby *et al.* 2002).

Our first objective was to test for intercontinental differences in grazing-resistance traits. Based on these differences, we made inferences about the relative intensities of evolutionary history of grazing in sagebrush and Patagonian steppe, and generated predictions about the effects of domestic livestock grazing on these ecosystems. Our second objective was to test the prediction from Milchunas, Sala & Lauenroth (1988) that aridity favours the development of grazing resistance. This test focused on differences between the dry and wet sites within each ecosystem.

## Materials and 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. Similar parent material, derived from basalt lava flows and granitic intrusions, occur in the southern Andes and the Cascades (Engelbreton, Cox & Gordon 1985; Ramos 1989). The climate in both regions is characterized by warm, dry summers and cool, wet winters. 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 this gradient of decreasing precipitation, with forests giving way to grasslands and then grass-shrub steppe.

Despite the similarity in climate at the macro scale (Paruelo *et al.* 1995), detailed comparison reveals subtle but potentially important differences (Adler 2003). First, while the seasonal distribution of rainfall is quite similar, the limited land mass of temperate South America allows a stronger maritime influence; Patagonian sites typically have less thermal amplitude, with milder winters and cooler summers, than sites in sagebrush steppe (Box 2002) (Fig. 2). Secondly, 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 larger in Patagonia than in the sagebrush steppe. Finally, winds are stronger in Patagonia, averaging more than 20 km h<sup>-1</sup> during the

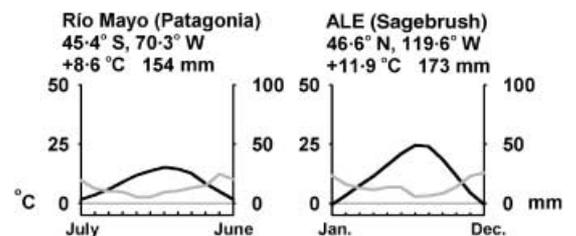


Fig. 2. Mean monthly precipitation and temperature for dry sites in Patagonia (Beltrán 1997) and the sagebrush steppe (Hoitink, Burk & Ramsdell 1999). The black, concave-down line shows temperature, the grey line precipitation. ALE, Arid Lands Ecology Reserve.

growing season (Beltrán 1997) compared with an average of below 10 km h<sup>-1</sup> in sagebrush steppe (Hoitink, Burk & Ramsdell 1999), and contribute to the region's aridity (Soriano 1983).

We selected two study sites in Patagonia and two in sagebrush steppe, one in the arid zone co-dominated by grasses and shrubs and the other at the grass-dominated, subhumid to semi-arid portion of the precipitation gradient. The dry sagebrush steppe site was Wanapum State Park, near the town of Vantage, WA (47°N, 120°W, 300 m a.s.l.). Soils are unglaciated silty loams. Mean annual precipitation is approximately 175 mm and mean annual temperature 12 °C (based on data from the Arid Lands Ecology Reserve, shown in Fig. 2). The dominant species are *Agropyron spicatum* and the shrub *Artemisia tridentata* var. *tridentata* (botanical nomenclature follows Hitchcock & Cronquist 1973), representative of the most widespread sagebrush steppe community type (Küchler 1964; Daubenmire 1970). We refer to these two vegetation types collectively as sagebrush steppe. The wet sagebrush steppe site was located west of the town of Grand Coulee, WA (approximately 48°N and 119.3°W and 800 m a.s.l.), on glaciated silty loam soils. Mean annual precipitation is at least 300 mm (Daly, Neilson & Phillips 1994; data from local ranchers) and mean annual temperature 7.5 °C (based on data from nearby Waterville, WA). 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.

The dry Patagonia site was 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 a.s.l.). 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 spinosum*, *Adesmia campestris* and *Senecio filaginoides* (botanical nomenclature follows Correa 1969–1999). The wet Patagonia site was located in south-west Chubut province, Argentina (46°S, 71.5°W, 650 m a.s.l.), on glaciated silty loam soils. Mean annual precipitation is 400 mm (data from local rancher) and mean annual temperature is 6.5 °C (data from Balmaceda, Chile). Vegetation, corresponding to the subAndean grass steppe community (León *et al.* 1998), is dominated by the perennial bunchgrass *Festuca palleescens* and the most common shrub is *Mulinum spinosum*.

#### GRAZING-RESISTANCE TRAITS

The traits we measured fell into two categories: morphological and chemical. We measured morphological traits related to stature (Table 1), such as the vertical height above the ground of inflorescences and leaves,

**Table 1.** List of measured traits with their units and abbreviations. Tissue concentration data are based on biomass dry weight

Code	Trait	Units
LEAF HT	Leaf height above ground	cm
FLWR HT	Inflorescence height	cm
LEAF W1	Leaf width	mm
LEAF W2	Leaf thickness	mm
BLADE*	Length of leaf blade	cm
SHEATH	Length of leaf sheath	cm
FORCE	Leaf tensile strength	Newtons mm <sup>-2</sup>
VEGREPR	Vegetative reproduction	Categorical (yes, no)
CELLSOLS	Cell solubles	g g <sup>-1</sup>
HEMICELL* <sup>*</sup>	Hemicellulose	g g <sup>-1</sup>
CELLUL	Cellulose	g g <sup>-1</sup>
LIGNIN	Lignin	g g <sup>-1</sup>
ASH	Ash	g g <sup>-1</sup>
C	Carbon	%
N	Nitrogen	%
SI	Silica	mg kg <sup>-1</sup>
P	Phosphorus	mg kg <sup>-1</sup>

\*Traits were excluded from the PCA to reduce collinearity.

because short plants should avoid grazing better than tall plants. Other morphological traits included the potential for vegetative reproduction, which may be related to tolerance as much as avoidance, and leaf tensile strength, which correlates with measures of palatability and digestibility (Cornelissen *et al.* 1999). The chemical traits we measured (Table 1) described the forage quality of each species, and included digestible and non-digestible fibre components, carbon (C), nitrogen (N) and phosphorus (P). We also measured silica (Si), reported to function as a defence against herbivory (McNaughton *et al.* 1985).

#### FIELD METHODS

We measured resistance traits on all graminoids common to each study site. In order to minimize the confounding effects of variation in grazing intensity, we used plants from long-term exclosures at the dry Patagonia and sagebrush steppe sites, and within recent (1-year-old) exclosures located in rarely grazed areas in the wet Patagonia steppe site. Thus, the comparison focused on ungrazed plants only, and not on differences between grazed and ungrazed plants of each species.

We measured morphological traits and collected above-ground biomass during 2001, near the end of each species' growing season as seeds began to harden but well before senescence (January in Patagonia, May and June in sagebrush steppe). Some early phenology species, such as *Poa secunda* in the sagebrush steppe, were harvested well before later-maturing species. To measure leaf tensile strength we built a spring-tensioned device modelled on Hendry & Grime (1993). Immediately after collecting biomass, we placed mature green leaves in water to prevent desiccation. We measured the

force required to tear a single leaf, with 10 replicates for each species. Because leaves on these graminoids rarely have an obvious widest point, we measured leaf width and thickness at the point of breakage, then expressed tensile strength as force (Newtons) over leaf cross-section ( $\text{mm}^2$ ). We measured all remaining physical traits (Table 1) on the individual plant of each species growing nearest each of 10 predetermined points on a line transect. The trait values for each species used in the analysis were the means of these 10 measurements. After measuring physical traits, we harvested all 10 plants of each species, and additional biomass if necessary, for subsequent laboratory analysis of general leaf chemistry (Table 1).

To prepare plant tissue samples for chemical analysis, we separated 5 g of mature green leaves (blades and sheaths) of each species from each site and dried the sample for 48 h at 55 °C. Each sample was ground in a Wiley mill with a 1-mm screen. We used the van Soest (1982) method for fibre analysis, and sent the samples to the CSU Soil and Plant Testing Laboratory (Fort Collins, CO, USA) 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 & Kotuby-Amacher 1996).

#### STATISTICAL ANALYSIS

The purpose of the statistical analysis was twofold: (i) to detect overall (multivariate) differences in graminoid traits within and between regions, and (ii) to identify key individual traits and compare their mean values across regions. We performed a principal components analysis (PCA) on the samples by traits matrix to describe overall (multivariate) variation in traits (Canoco 4.0 1998). We chose PCA rather than discriminant analysis because our objective was to assess differences among species along the most important dimensions of trait variation, rather than simply differentiate species from different sites. We then compared species' scores on the primary PCA axes, treating these scores as indicators of composite trait differences. To test for differences between Patagonian (PAT) and sagebrush steppe (SGBR) plants, we used 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-site differences, we used Tukey honest significant differences (HSD), setting  $\alpha = 0.05$ . We repeated these tests considering only the scores of the three most abundant species at each site. We defined the dominant species based on basal cover data collected across grazing intensity gradients at each site (Adler 2003), choosing the two graminoids most abundant in long-term ungrazed sites along with the strongest grazing increaser.

The PCA also served to identify individual traits of particular importance in explaining variation among species. We performed similar two-factor ANOVAS on

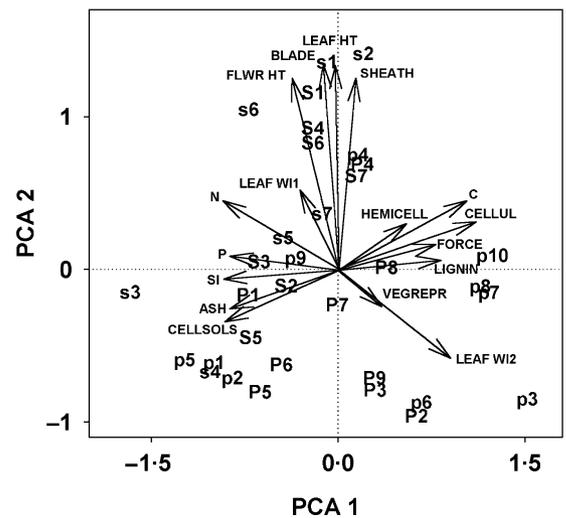


Fig. 3. Results from the PCA. Solid lines show the loading of traits (trait abbreviations listed in Table 1) and points show the scores of individual species from each site (species codes are defined in Table 3).

the values of these traits to test for differences among regions and sites.

Note that in both sagebrush steppe and Patagonia some species occurred in both dry and wet sites, raising a question about independence of samples and resulting inflation of sample size in contrasts on aridity. We justified treating such samples as independent because of differences in morphology between study areas, which may indicate separate genotypes (Kotani & Bergelson 2000). Furthermore, when we removed samples of duplicate species from the site where they were least abundant, the results of ANOVAS on PCA 1 and 2 scores did not change (we could not repeat this test for the dominants-only case as removing duplicates made sample sizes too small).

#### Results

The first PCA axis (PCA 1) was correlated with traits related to palatability and digestibility, such as C, lignin and leaf tensile strength, which increased along the axis, and cell solubles, N and P, which decreased on the axis (Fig. 3). Si, low among all species, with values ranging from 18 to 322 p.p.m., also decreased along this axis. The second axis (PCA 2) was positively correlated with measures of plant stature, such as leaf and flower height (Fig. 3). The first three ordination axes explained 30.0%, 20.9% and 10.7% 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 (Table 2) when only the dominant three species from each site were considered. Region and the region  $\times$  precipitation interaction were both significant. *Post-hoc* comparisons showed that species from the Patagonian dry site had significantly higher scores on PCA 1 than species from any other

**Table 2.** Results of two-way ANOVAs on PCA axis 1 and 2 scores, using either all species or only dominant species. Significant *P* values are shown in bold.

Source	Sum of squares	d.f.	<i>F</i>	<i>P</i>
PCA axis 1, all species				
Region	2.219	1	4.221	<b>0.049</b>
Precipitation	0.031	1	0.060	0.809
Region × precipitation	0.587	1	1.118	0.300
Error	15.241	29		
PCA axis 1, dominant species				
Region	3.172	1	35.207	<b>&lt; 0.001</b>
Precipitation	0.407	1	4.513	0.066
Region × precipitation	0.877	1	9.734	<b>0.014</b>
Error	0.721	8		
PCA axis 2, all species				
Region	4.342	1	11.882	<b>0.002</b>
Precipitation	0.153	1	0.418	0.523
Region × precipitation	0.0001	1	0.0002	0.990
Error	0.365	29		
PCA axis 2, dominant species				
Region	0.583	1	1.209	0.303
Precipitation	0.024	1	0.049	0.831
Region × precipitation	0.023	1	0.047	0.835
Error	3.859	8		

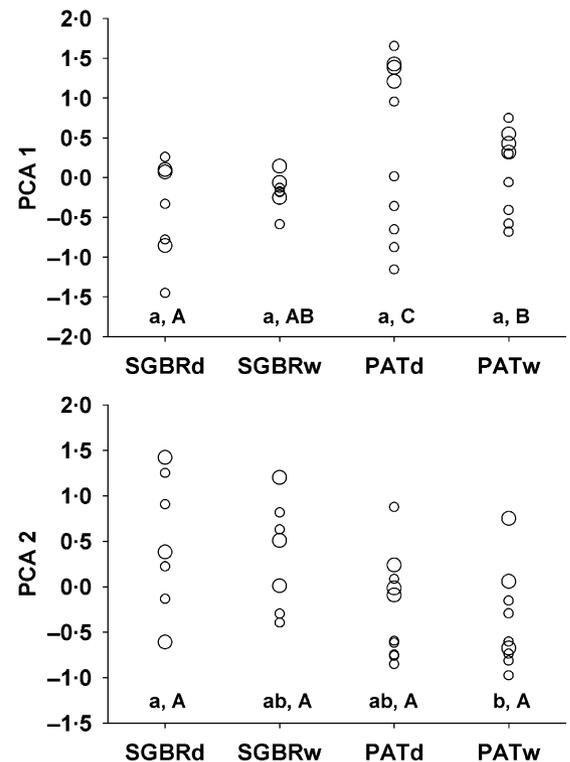
site, indicating lower quality leaf tissue, and species from the Patagonia wet site had higher scores than species from the sagebrush steppe dry site (Fig. 4). The ANOVA on PCA 2 scores was significant when all species were included (Table 2), due to a strong difference between regions: Patagonian species tended to be shorter than sagebrush steppe species (Fig. 4). However, when we considered only dominant species, the ANOVA was not significant (Table 2).

The PCA identified certain traits of particular importance in explaining total variation among species: C, N and cellulose had the highest loadings on PCA 1, and leaf height and flower height scored high on PCA 2. ANOVAs on the values of these individual traits (listed in Table 3) showed that Patagonian graminoid species were significantly lower in N ( $F = 30.8$ ,  $P \leq 0.001$ ), had higher C : N ratios ( $F = 18.9$ ,  $P \leq 0.001$ ) and shorter inflorescences ( $F = 14.4$ ,  $P \leq 0.001$ ) and leaves ( $F = 14.2$ ,  $P \leq 0.001$ ) than species from sagebrush steppe. These differences in stature, however, were not significant among the dominant species. In contrast, values for cellulose concentration were not significantly different when all species were compared, but were significantly higher for Patagonian species when only dominant species were considered ( $F = 15.1$ ,  $P = 0.005$ ).

## Discussion

### EVIDENCE FOR A MORE INTENSE HISTORY OF GRAZING IN PATAGONIA

Our analysis of grazing-resistance traits provides evidence supporting the hypothesis that grazing has been



**Fig. 4.** Between-site differences in PCA scores. Individual species' scores are shown (larger symbols indicate dominant species) on PCA axes 1 (a) and 2 (b). SGBRd and SGBRw = sagebrush steppe dry and wet study sites; PATd and PATw = Patagonian steppe dry and wet study sites. Letters indicate significant differences between means for each site (Tukey HSD,  $\alpha < 0.05$ ). Lowercase letters refer to contrasts among means for all species, uppercase for means of dominant species only.

a stronger selective pressure in Patagonian steppe than in sagebrush steppe. Patagonian graminoids, especially the dominants at the driest site, have leaves that are lower in N and higher in fibre than leaves of sagebrush steppe dominants. Patagonian species are also shorter, although this difference is minimized when only dominants are considered.

To argue that such differences in traits are evidence for a more intense grazing history in Patagonia assumes that poor-quality leaves are an effective defence against herbivores. Herbivores do, in fact, avoid plants that are difficult to digest (and decompose) in favour of their more palatable competitors (Grime *et al.* 1996; Augustine & McNaughton 1998). This type of avoidance is further enhanced by tough leaves that result in large quantities of standing dead biomass, which even large herbivores avoid (Cruz, Ganskopp & Vavra 1998). The dominant *Stipa speciosa* at the dry Patagonia site retains four times more standing dead biomass than *Agropyron spicatum* at an arid sagebrush site (Soriano 1976; Rickard *et al.* 1988).

Our comparison of graminoids from sagebrush and Patagonian steppe allows us to make statements only about their relative degree of adaptation to grazing. To provide a broader perspective, we can use graminoids from the shortgrass steppe, a classic example of a

**Table 3.** List of species from each site and values for selected traits (leaf and inflorescence height in cm, N in percentage). Dominant species are shown in bold

Region	Precipitation	Species code	Species name	Leaf height	Inflorescence height	N	C/N
Sagebrush	Dry (175 mm)	s1	<i>Agropyron spicatum</i>	37	59	1.04	41.2
		s2	<i>Orizhopsis hymenoides</i>	33	52	1.43	31.2
		s3	<i>Poa cusickii</i>	18	42	1.67	23.4
		s4	<b><i>Poa secunda</i></b>	6	31	1.52	28.0
		s5	<i>Sitanion hystrix</i>	16	29	1.73	25.3
		s6	<i>Stipa comata</i>	28	60	1.89	22.9
		s7	<b><i>Stipa thurberiana</i></b>	26	39	1.26	33.5
			Mean (all species)	23	44	1.51	29.3
			Mean (dominants)	23	43	1.27	34.2
		Sagebrush	Wet (300 mm)	S1	<b><i>Agropyron spicatum</i></b>	35	46
S2	<i>Carex filifolia</i>			20	21	1.68	26.0
S3	<b><i>Festuca idahoensis</i></b>			25	36	1.09	37.2
S4	<i>Poa juncifolia</i>			29	46	1.22	35.8
S5	<i>Poa secunda</i>			7	29	1.65	26.1
S6	<i>Stipa nelsonii</i>			28	41	1.69	26.1
S7	<b><i>Stipa comata</i></b>			21	34	1.63	27.1
	Mean (all species)			23	36	1.49	29.8
	Mean (dominants)			27	39	1.40	31.6
Patagonia	Dry (154 mm)			p1	<i>Bromus pictus</i>	9	19
		p2	<i>Bromus setifolius</i>	11	17	1.05	37.3
		p3	<i>Carex andina</i>	5	1	0.76	59.2
		p4	<i>Festuca argentina</i>	28	51	1.11	39.5
		p5	<i>Hordeum comossum</i>	10	20	1.22	31.8
		p6	<i>Poa lanuginosa</i>	9	19	0.71	59.9
		p7	<b><i>Poa ligularis</i></b>	18	22	0.73	61.9
		p8	<b><i>Stipa humilis</i></b>	17	23	0.77	59.6
		p9	<i>Stipa psylantha</i>	19	35	1.07	38.2
		p10	<b><i>Stipa speciosa</i></b>	19	29	0.72	63.5
			Mean (all species)	15	24	0.93	48.5
	Mean (dominants)	18	25	0.74	61.7		
Patagonia	Wet (400 mm)	P1	<i>Bromus pictus</i>	12	27	1.34	30.7
		P2	<i>Carex andina</i>	3	1	0.97	45.3
		P3	<b><i>Festuca magellanica</i></b>	6	21	0.77	57.4
		P4	<b><i>Festuca pallescens</i></b>	25	48	0.98	43.6
		P5	<i>Hordeum comossum</i>	13	27	1.54	26.3
		P6	<i>Koeleria grisebachii</i>	5	20	1.32	32.3
		P7	<i>Luzula chilensis</i>	6	29	1.14	39.2
		P8	<b><i>Poa ligularis</i></b>	16	31	0.90	48.3
		P9	<i>Rhytidosperra picta</i>	5	4	1.16	36.4
			Mean (all species)	10	23	1.13	39.9
	Mean (dominants)	16	33	0.88	49.7		

semi-arid system with an intense evolutionary history of grazing (Milchunas *et al.* 1989). Measurements of the same traits used in this study on common species in shortgrass steppe showed that, in terms of forage quality, shortgrass steppe graminoids are similar to those from the wet Patagonia site, have higher quality than those from arid Patagonia, but lower quality than sagebrush steppe species (Adler 2003). In terms of plant stature, the shortgrass species were intermediate, larger than Patagonian species but smaller than sagebrush species (Adler 2003). Although these results further support the case for a long evolutionary history of grazing in Patagonia, we caution that this interpretation is confounded by important differences in climate; many of the shortgrass species have C<sub>4</sub> photosynthesis, whereas all the species that we assessed from Patagonian and sagebrush steppe have C<sub>3</sub>.

Morphological plasticity may be an important strategy that plants use to avoid grazing (McIntyre *et al.* 1999). For example, some grazing-adapted grasses adopt a prostrate growth habit in response to grazing (Hickey 1961). Our analysis did not include measurements of changes in plant growth form following defoliation. Field observations, however, suggested that Patagonian but not sagebrush graminoids may possess such morphological plasticity. While leaf and flower height of the sagebrush dominant *Agropyron spicatum* is relatively constant, heavily grazed individuals of an arid Patagonian dominant, *Poa ligularis*, adopt a prostrate growth form. When grown in the glasshouse, differences between the short and tall forms of *Poa ligularis* disappeared (P.B. Adler, personal observation), indicating that these forms do not represent distinct genotypes. This anecdotal evidence of plasticity, consistent with

a longer evolutionary history of grazing in Patagonia, deserves further study.

Although Si has been reported to function as a defence against grazing (McNaughton *et al.* 1985), we found that Si values were positively correlated with palatability, as measured by the first ordination axis. This positive relationship between Si and palatability, also observed in previous studies (Cid *et al.* 1990), suggests that Si, at least at the low levels found in these sagebrush and Patagonian steppe grasses, is not an effective anti-herbivore defence.

#### ARIDITY

Milchunas, Sala & Lauenroth (1988) predicted that arid conditions promote the development of grazing-resistance traits. The trait differences between the dry and wet sites in Patagonia were consistent with this prediction: dominant species from the dry site had higher scores on PCA 1, suggesting lower forage quality and better grazing resistance. Other research from Patagonia offers supporting evidence. Austin & Sala (2002) showed that leaf N content increased with precipitation across an even wider range of moisture. In a study of phenotypic variation, Oliva *et al.* (1993) found that *Festuca pallezensis* growing in dry areas of Patagonia had shorter, tougher leaves than plants growing in more humid environments. At least in Patagonia, aridity appears to favour grazing-avoidance traits, while tolerance traits, such as higher leaf N, increase with precipitation. The lack of significant differences in traits across the sagebrush precipitation gradient may reflect the smaller difference in mean annual precipitation between the two sagebrush sites (*c.* 125 mm) compared with the differences between the two Patagonian sites (*c.* 250 mm), although other environmental covariates, such as soil texture, could also be involved (see below).

#### ALTERNATIVE EXPLANATIONS

Although the differences in resistance 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. The Patagonian steppe experiences stronger winds than sagebrush steppe, perhaps selecting for shorter stature and stiffer leaves. The larger area of true aridity in Patagonia suggests another alternative explanation: the arid areas that do occur in the sagebrush steppe may be too small to isolate effectively drought-tolerant genotypes from surrounding conspecifics, preventing local adaptation.

While wind or the distribution of aridity could play a role in explaining patterns of variation in plant traits, the best alternative explanation involves soils. N limitation created by extremely coarse soils can explain differences in forage quality between regions, as well as differences within Patagonia. The soils at the dry Patagonian field site were extremely coarse, with sand

content more than 90%, whereas at the wet Patagonia site sand content ranged from 67% to 89%. Sand content was lower at both sagebrush sites, ranging from 42% to 66% and 41% to 73% at the dry and wet sites, respectively (Adler 2003). Coarse soils accumulate less N than finer textured soils because of less stabilization of N through adsorption and aggregation onto clays (Schimel, Stillwell & Woodmansee 1985; Schimel, Coleman & Horton 1985; Barrett & Burke 2002). Indeed, arid Patagonian soils contained much less total N than soils from the arid sagebrush study area, despite similar levels of above-ground production (Adler 2003). Soil N concentrations in bare ground microsites at the dry Patagonian site averaged 0.03%, compared with 0.07% at the dry sagebrush site. Relative differences between the wet sites were smaller, with average N concentrations of 0.17% and 0.21% in Patagonian and sagebrush steppe, respectively (Adler 2003). A negative relationship between soil sand fraction and N availability could explain why the Patagonian graminoids have lower N concentrations than the sagebrush species, and also why N concentrations in dominant species varied more strongly between dry and wet sites in Patagonian than in sagebrush steppe.

Finally, we cannot ignore the possibility that the poor-quality graminoids of Patagonia are a legacy of evolutionary factors much further in their past. 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 & Denton 1987). Perhaps differences in the early environments of these species imposed selective pressures that continue to constrain their 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 grazing-resistance traits of graminoids from Patagonia and the sagebrush steppe suggest that the introduction of domestic livestock will have different effects in these ecosystems. The presence of both palatable and extremely unpalatable graminoids in arid Patagonia means that grazing should cause large changes in relative abundance within this functional group, but few changes in overall graminoid 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 total abundance of perennial grasses (Soriano 1976). In the sagebrush steppe, grazing causes dramatic decreases in the abundance of perennial grasses as a group (Mueggler 1950; Laycock

1967; Rickard *et al.* 1975). Plant communities in sub-humid Patagonia respond more similarly to the sagebrush steppe, with decreases in overall grass abundance (León & Aguiar 1985). The different responses at the wet and dry Patagonian sites should be expected given their different ranges in forage quality.

A second implication of poor forage quality in Patagonia has to do with its negative effects on secondary production. When crude protein content of forage 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). Estimating crude protein as 6.25 times the N concentration, all the dominant species at the dry Patagonia site fall below this threshold, with N content in late growing season live leaf tissue ranging from 4.5% to 4.8%, and a mean N content for all species of 5.8% (Table 3). These low N content values were confirmed by similar values in the samples collected the previous year (data not shown) and by other studies in Patagonia (reviewed by Borelli 2001). Crude protein 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 7.9% and 8.8%, respectively (Table 3), consistent with published values (Murray, Mayland & van Soest 1978; Ganskopp & Bohnert 2001).

If poor forage quality is limited to only a few species, or to subordinate species, ruminants can sustain high intake rates by foraging selectively (Hobbs & Swift 1985). But when the dominant plant species at a site all have low crude protein contents and the abundance of higher quality species is low, as at the dry Patagonia site, forage quality should negatively affect herbivore populations. Demonstrating 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. By limiting potential stocking rates, poor forage quality may reduce the Patagonian steppe'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 & Thompson 1982; Milchunas, Sala & Lauenroth 1988). Is it still useful? When the objective is to predict the current response of plant communities to grazing, we may only need information on plant traits. However, 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 selective pressures, including the evolutionary history of grazing. Understanding why different plant traits evolved in different ecosystems will require careful

consideration of the role of the evolutionary history of grazing and its interaction with abiotic factors. Our comparison of sagebrush and Patagonian steppe suggests that abiotic factors influencing N availability, such as soil texture, deserve special attention.

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#### References

- Adler, P.B. (2003) *A comparison of livestock grazing effects on sagebrush steppe, USA and Patagonian steppe, Argentina*. PhD Dissertation. Colorado State University, Fort Collins, CO.
- Allison, C.D. (1985) Factors affecting forage intake by range ruminants: a review. *Journal of Range Management*, **38**, 305–311.
- Anderson, V. & Briske, D.D. (1995) Herbivore-induced species replacement in grasslands: is it driven by herbivory tolerance or avoidance? *Ecological Applications*, **5**, 1014–1024.
- Augustine, D.J. & McNaughton, S.J. (1998) Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management*, **62**, 1165–1183.
- Austin, A.T. & Sala, O.E. (2002) Carbon and nitrogen dynamics across a natural precipitation gradient in Patagonia, Argentina. *Journal of Vegetation Science*, **13**, 351–360.
- Barrett, J.E. & Burke, I.C. (2002) Nitrogen retention in semiarid ecosystems across a soil organic matter gradient. *Ecological Applications*, **12**, 878–890.
- Beltrán, A. (1997) *Caracterización microclimática del distrito occidental de la estepa Patagónica*. Masters Thesis. Universidad de Buenos Aires, Buenos Aires, Argentina.
- Bock, J.H., Jolls, C.L. & Lewis, A.C. (1995) The effects of grazing on alpine vegetation: a comparison of the central Caucasus, Republic of Georgia, with the Colorado Rocky Mountains, USA. *Arctic and Alpine Research*, **27**, 130–136.
- Borelli, P. (2001) Producción animal sobre pastizales naturales. *Ganadería Ovina Sustentable en la Patagonia Austral* (eds P. Borrelli & G. Oliva), pp. 129–159. INTA, Santa Cruz, Argentina.
- Box, E.O. (2002) Vegetation analogs and differences in the northern and southern hemispheres: a global comparison. *Plant Ecology*, **163**, 139–154.
- Burkhardt, J.W. (1996) *Herbivory in the Intermountain West: An Overview of Evolutionary History, Historic Cultural Impacts and Lessons from the Past*. Station Bulletin 58. Idaho Forest, Wildlife and Range Experiment Station, University of Idaho, Idaho.
- Cid, M.S., Detling, J.K., Whicker, A.D. & Brizuela, M.A. (1990) Silicon uptake and distribution in *Agropyron smithii* as related to grazing history and defoliation. *Journal of Range Management*, **43**, 344–346.
- Cornelissen, J.H.C., Perez-Harguindeguy, N., Díaz, S., Grime, J.P., Marzano, B., Cabido, M., Vendramini, F. & Cerabolini, B. (1999) Leaf structure and defence control litter decomposition rate across species and life forms in

- regional floras on two continents. *New Phytologist*, **143**, 191–200.
- Correa, M.V. (1969–1999) *Flora Patagónica, Volumes I–VII*. Instituto Nacional de Tecnología Agropecuaria, Buenos Aires, Argentina.
- Coughenour, M.B. (1985) Graminoid responses to grazing by large herbivores: adaptations, exaptations and interacting processes. *Annals of the Missouri Botanical Garden*, **72**, 852–863.
- Cruz, R., Ganskopp, D. & Vavra, M. (1998) *Modeling Habitat Preferences of Cattle on Eastern Oregon Rangelands*. Eastern Oregon Agricultural Research Center Annual Report 1998, Special Report 991. Agricultural Research Station, Oregon State University, Oregon.
- Daly, C., Neilson, R.P. & Phillips, D.L. (1994) A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *Journal of Applied Meteorology*, **33**, 140–158.
- Daubenmire, R. (1970) *Steppe Vegetation of Washington*. Technical Bulletin 62. Washington Agricultural Station, College of Agriculture, Washington State University, Washington.
- Daubenmire, R. (1975) Floristic plant geography of eastern Washington and northern Idaho. *Journal of Biogeography*, **2**, 1–18.
- Díaz, S., Acosta, A. & Cabido, M. (1992) Morphological analysis of herbaceous communities under different grazing regimes. *Journal of Vegetation Science*, **3**, 689–696.
- Díaz, S., Acosta, A. & Cabido, M. (1994) Community structure in montane grasslands of central Argentina in relation to land use. *Journal of Vegetation Science*, **5**, 483–488.
- Díaz, S., Noy-Meir, I. & Cabido, M. (2001) Can grazing response of herbaceous plants be predicted from simple vegetative traits? *Journal of Applied Ecology*, **38**, 497–508.
- Engelbreton, D.C., Cox, A. & Gordon, R.G. (1985) *Relative Motions Between Oceanic and Continental Plates in the Pacific Basin*. Special Paper 206. Geological Society of America, Boulder, CO.
- Franklin, W.L. (1981) Biology, ecology, and relationship to man of the South American camelids. *Mammalian Biology in South America* (eds M.A. Mars & H.H. Genoways), pp. 457–489. Special Publication Series. University of Pittsburgh, Pittsburgh, MA.
- Ganskopp, D. & Bohnert, B. (2001) Nutritional dynamics of 7 northern Great Basin grasses. *Journal of Range Management*, **54**, 640–647.
- Golluscio, R.A., Paruelo, J.M., Mercau, J.L. & Deregibus, V.A. (1998) Urea supplementation effects on the utilization of low-quality forage and lamb production in Patagonian rangelands. *Grass and Forage Science*, **53**, 47–56.
- Gould, S.J. & Lewontin, R.C. (1979) The spandrels of San Marcos and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London B*, **205**, 581–598.
- Grass Phylogeny Working Group (2001) Phylogeny and subfamilial classification of the grasses (Poaceae). *Annals of the Missouri Botanical Garden*, **88**, 373–457.
- Grime, J.P., Cornelissen, J.H.C., Thompson, K. & Hodgson, J.G. (1996) Evidence of a causal connection between anti-herbivore defence and the decomposition rate of leaves. *Oikos*, **77**, 489–494.
- Hendon, B.C. & Briske, D.D. (2002) Relative herbivory tolerance and competitive ability in two dominant : subordinate pairs of perennial grasses in a native grassland. *Plant Ecology*, **160**, 43–51.
- Hendry, G.A.F. & Grime, J.P. (1993) *Methods in Comparative Plant Ecology*. Chapman & Hall, London, UK.
- Hickey, W.C. Jr (1961) Growth form of crested wheatgrass as affected by site and grazing. *Ecology*, **42**, 173–176.
- Hitchcock, C.L. & Cronquist, A. (1973) *Flora of the Pacific Northwest: An Illustrated Manual*. University of Washington Press, Seattle, WA.
- Hobbs, N.T. & Swift, D.M. (1985) Estimates of habitat carrying capacity incorporating explicit nutritional constraints. *Journal of Wildlife Management*, **49**, 814–822.
- Hoitink, D.J., Burk, K.W. & Ramsdell, J.V. (1999) *Hanford Site Climatological Summary 1998 with Historical Data*. PNNL-12087. Pacific Northwest National Laboratory, Richland, WA.
- de Jong, T.J. & van der Meijden, E. (2000) On the correlation between allocation to defence and regrowth in plants. *Oikos*, **88**, 503–508.
- Kotaniemi, P.M. & Bergelson, J. (2000) Effects of simulated grazing on different genotypes of *Bouteloua gracilis*: how important is morphology? *Oecologia*, **123**, 66–74.
- Küchler, A.W. (1964) *Potential Natural Vegetation of the Conterminous United States*. Special Publication No. 36. American Geographical Society, New York, NY.
- Larson, F. (1940) The role of bison in maintaining the short grass plains. *Ecology*, **21**, 113–121.
- Lauenroth, W.K. (1998) Guanacos, spiny shrubs and the evolutionary history of grazing in the Patagonian steppe. *Ecologia Austral*, **8**, 211–216.
- Lavorel, S., McIntyre, S. & Grigulis, K. (1999) Plant response to disturbance in a Mediterranean grassland: how many functional groups? *Journal of Vegetation Science*, **10**, 661–672.
- Laycock, W.A. (1967) How heavy grazing and protection affect sagebrush–grass ranges. *Journal of Range Management*, **20**, 206–213.
- León, R.C.J. & Aguiar, M.R. (1985) El deterioro por uso pastoral en estepas herbáceas patagónicas. *Phytocoenologia*, **13**, 181–196.
- León, R.C.J., Bran, D., Collantes, M., Paruelo, J.M. & Soriano, A. (1998) Grandes unidades de vegetación de la Patagonia extra andina. *Ecologia Austral*, **8**, 125–144.
- Leopold, E.B. & Denton, M.F. (1987) Comparative age of grassland and steppe east and west of the northern Rocky Mountains. *Annals of the Missouri Botanical Garden*, **74**, 841–867.
- Lyman, R.L. & Wolverton, S. (2002) The late prehistoric–early historic game sink in the northwestern United States. *Conservation Biology*, **16**, 73–85.
- McIntyre, S. & Lavorel, S. (2001) Livestock grazing in subtropical pastures: steps in the analysis of attribute response and plant functional types. *Journal of Ecology*, **89**, 209–226.
- McIntyre, S., Lavorel, S., Landsberg, J. & Forbes, T.D.A. (1999) Disturbance response in vegetation towards a global perspective on functional traits. *Journal of Vegetation Science*, **10**, 621–630.
- Mack, R.N. & Thompson, J.N. (1982) Evolution in steppe with few large, hooved mammals. *American Naturalist*, **119**, 757–773.
- McNaughton, S.J., Tarrants, J.L., McNaughton, M.M. & Davis, R.H. (1985) Silica as a defence against herbivory and a growth promoter in African grasses. *Ecology*, **66**, 528–535.
- van der Meijden, E., Wijn, M. & Verkaar, H.J. (1988) Defence and regrowth, alternative plant strategies in the struggle against herbivores. *Oikos*, **51**, 355–363.
- Milchunas, D.G. & Lauenroth, W.K. (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, **63**, 327–366.
- Milchunas, D.G., Lauenroth, W.K., Chapman, P.L. & Kazempour, M.K. (1989) Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. *Vegetatio*, **80**, 11–23.
- Milchunas, D.G., Sala, O.E. & Lauenroth, W.K. (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist*, **132**, 87–106.
- Miller, R.O. & Kotuby-Amacher, J. (1996) *Western States Laboratory Proficiency Testing Program, Soil and Plant*

- Analytical Methods, Version 3-0*. Colorado State University and Utah State University, USA.
- Mueggler, W.F. (1950) Effects of spring and fall grazing by sheep on vegetation of the Upper Snake River Plains. *Journal of Range Management*, **3**, 308–315.
- Murray, R.B., Mayland, H.F. & van Soest, P.J. (1978) *Growth and Nutritional Value to Cattle of Grasses on Cheatgrass Range in Southern Idaho*. Research Paper INT-199. USDA Forest Service, Ogden, UT.
- Oliva, G., Martinez, A., Collantes, M. & Dubcovsky, J. (1993) Phenotypic plasticity and contrasting habitat colonization in *Festuca pallescens*. *Canadian Journal of Botany*, **71**, 970–977.
- Paruelo, J.M., Jobbagy, E.G., Sala, O.E., Lauenroth, W.K. & Burke, I.C. (1998) Functional and structural convergence of temperate grassland and shrubland ecosystems. *Ecological Applications*, **8**, 194–206.
- Paruelo, J.M., Lauenroth, W.K., Epstein, H.E., Burke, I.C. & Aguiar, M.R. (1995) Regional climatic similarities in the temperate zones of North and South America. *Journal of Biogeography*, **22**, 915–925.
- Ramos, V.A. (1989) The birth of South America. *American Scientist*, **77**, 444–450.
- Redak, R.A. (1987) Forage quality: secondary chemistry of grasses. *Integrated Pest Management: A Shortgrass Prairie Perspective* (ed. J.L. Capinera), pp. 38–55. Westview Press, Boulder, CO.
- Rickard, W.H., Rogers, L., Vaughan, B.E. & Liebetrau, S.F. (1988) *Shrub-Steppe: Balance and Change in a Semi-Arid Terrestrial Ecosystem*. Elsevier, Amsterdam, the Netherlands.
- Rickard, W.H., Uresk, D.W. & Cline, J.F. (1975) Impact of cattle grazing on three perennial bunchgrasses in south-central Washington. *Journal of Range Management*, **28**, 108–112.
- Schimel, D.S., Coleman, D.C. & Horton, K.A. (1985b) Soil organic matter dynamics in paired rangeland and cropland toposequences in North Dakota. *Geoderma*, **36**, 201–214.
- Schimel, D., Stillwell, M.A. & Woodmansee, R.G. (1985a) Biogeochemistry of C, N, and P in a soil catena of the shortgrass steppe. *Ecology*, **66**, 276–282.
- van Soest, P.J. (1982) *Nutritional Ecology of the Ruminant: Ruminant Metabolism, Nutritional Strategies, the Cellulolytic Fermentation, and the Chemistry of Forages and Plant Fibers*. O. & B. Books, Corvallis, OR.
- Solbrig, O.T. (1973) The origin and floristic affinities of the South American temperate desert and semidesert regions. *Evolution of Desert Biota* (ed. D.W. Goodall), pp. 7–49. University of Texas Press, Austin, TX.
- Soreng, R.J. (1990) Chloroplast-DNA phylogenetics and biogeography in a reticulating group: study in *Poa* (Poaceae). *American Journal of Botany*, **77**, 1383–1400.
- Soriano, A. (1976) *Ecología del pastizal de coirón amrgo (Stipa spp.) del sudoeste de Chubut*. Academia Nacional de Agronomía y Veterinaria, Buenos Aires, Argentina.
- Soriano, A. (1983) Deserts and semi-deserts of Patagonia. *Temperate Deserts and Semi-Deserts*. (ed. N.E. West), pp. 423–460. Ecosystems of the World Vol. 5. Elsevier, New York, NY.
- Stebbins, G.L. (1981) Coevolution of grasses and large herbivores. *Annals of the Missouri Botanical Garden*, **68**, 75–86.
- Strauss, S.Y. & Agrawal, A.A. (1999) The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology and Evolution*, **14**, 179–185.
- Vesk, P.A. & Westoby, M. (2001) Predicting plant species' responses to grazing. *Journal of Applied Ecology*, **38**, 897–909.
- Vesk, P.A., Leishman, M.R. & Westoby, M. (2004) Simple traits do not predict grazing response in Australian dry shrublands and woodlands. *Journal of Applied Ecology*, **41**, 22–31.
- Vicari, M. & Bazely, D.R. (1993) Do grasses fight back? The case for antiherbivore defences. *Trends in Ecology and Evolution*, **8**, 137–141.
- van Vuren, D. (1987) Bison west of the Rocky Mountains: an alternative explanation. *Northwest Science*, **61**, 65–69.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, **33**, 125–159.

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