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

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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

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; Diaz, Acosta & Cabido 1992; Lavorel, McIntyre & Grigulis 1999; McIntyre et al. 1999; Diaz, Noy-Meir & Cabido 2001; McIntyre & Lavorel 2001; Westoby et al. 2002), cross-system generalizations appear elusive (Vesk & Westoby 2001; Vesk, 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.

We can circumvent these problems by restating 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’.

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’.
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 (Engebretson, 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\(^{-1}\) during the
growing season (Beltrán 1997) compared with an average of below 10 km h$^{-1}$ 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 Rio 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 spectosa*, *Stipahumilis* 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 pallescens* 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, 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

![Table 1. List of measured traits with their units and abbreviations. Tissue concentration data are based on biomass dry weight.](image)
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 (mm²). 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 α = 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 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 (Kotanen & 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 × 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
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 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.

<table>
<thead>
<tr>
<th>Region</th>
<th>Precipitation</th>
<th>Species code</th>
<th>Species name</th>
<th>Leaf height</th>
<th>Inflorescence height</th>
<th>N</th>
<th>C/N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sagebrush</td>
<td>Dry (175 mm)</td>
<td>s1</td>
<td>Agropyron spicatum</td>
<td>37</td>
<td>59</td>
<td>1.04</td>
<td>41.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>s2</td>
<td>Orizopsis hymenoides</td>
<td>33</td>
<td>52</td>
<td>1.43</td>
<td>31.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>s3</td>
<td>Poa cusickii</td>
<td>18</td>
<td>42</td>
<td>1.67</td>
<td>23.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>s4</td>
<td>Poa secunda</td>
<td>6</td>
<td>31</td>
<td>1.52</td>
<td>28.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>s5</td>
<td>Sitanion hystrix</td>
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<td>29</td>
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<td>25.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>s6</td>
<td>Stipa comata</td>
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<td>22.9</td>
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<td></td>
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<td>Stipa thurberiana</td>
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<td>1.26</td>
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<tr>
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<td>23</td>
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<td>1.51</td>
<td>29.3</td>
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<tr>
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<td>Mean (dominants)</td>
<td>23</td>
<td>43</td>
<td>1.27</td>
<td>34.2</td>
<td></td>
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<td>Agropyron spicatum</td>
<td>35</td>
<td>46</td>
<td>1.46</td>
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<td></td>
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<td>1.68</td>
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<td></td>
<td></td>
<td>S3</td>
<td>Festuca idahoensis</td>
<td>25</td>
<td>36</td>
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<tr>
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<td>Poa secunda</td>
<td>7</td>
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<td>p1</td>
<td>Bromus pictus</td>
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<td>19</td>
<td>1.15</td>
<td>33.9</td>
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<td></td>
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<td>Bromus setifolius</td>
<td>11</td>
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<td>0.76</td>
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<td>1.11</td>
<td>39.5</td>
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<td>Poa lamigunosa</td>
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<td>Stipa humilis</td>
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<td></td>
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<td>0.74</td>
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<td>P1</td>
<td>Bromus pictus</td>
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<td>1.34</td>
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<td>Carex andina</td>
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<td>Festuca magellanica</td>
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<td>P7</td>
<td>Luzula chilensis</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>P8</td>
<td>Poa ligularis</td>
<td>16</td>
<td>31</td>
<td>0.90</td>
<td>48.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P9</td>
<td>Rhytidosperma picta</td>
<td>5</td>
<td>4</td>
<td>1.16</td>
<td>36.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mean (all species)</td>
<td>10</td>
<td>23</td>
<td>1.13</td>
<td>39.9</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mean (dominants)</td>
<td>16</td>
<td>33</td>
<td>0.88</td>
<td>49.7</td>
<td></td>
</tr>
</tbody>
</table>

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 C₄ photosynthesis, whereas all the species that we assessed from Patagonian and sagebrush steppe have C₃.

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 pallescens 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 con specifics, 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 Pooidae, 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...
Functional traits and grazing history

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 fell 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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