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Plant functional traits, herbivore selectivity and response to sheep grazing in Patagonian steppe grasslands

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Summary

1. In some ecosystems there is a positive feedback between forage quality and grazing intensity. This involves three components of plant tolerance to grazing: functional traits, herbivore selectivity and response to grazing. We analysed the relationships between these components at species and community levels in Patagonian steppe grasslands.

2. We measured plant functional traits [height, specific leaf area (SLA) and foliar toughness] and estimated sheep selectivity and grazing response indices for 35 plant species. Sheep selectivity indices were obtained from microhistological and species' availability data, and grazing response indices from species' abundances in sites with contrasting grazing intensities. We performed correlations and multiple regressions among the three types of variables across the pool of 35 species.

3. To analyse data at the community level, we computed weighted averages of traits and sheep selectivity indices for 34 floristic samples taken from each side of 17 fence lines with contrasting grazing intensities. Correlations between mean trait values and sheep selectivity across the 34 samples, and paired comparisons of those variables between sides of the fences, were performed.

4. Taller plants had leaves with lower SLA and/or higher toughness. Short species of intermediate toughness were selected more often by sheep, while SLA was not related to sheep selectivity. Short species with high SLA increased with grazing, while toughness and sheep selectivity were unrelated to grazing response.

5. At the community level, short swards with high average SLA had high selectivity indices and were more abundant on the most intensively grazed sides of fence lines. Leaf toughness was unrelated to other traits or to sheep selectivity, and showed no significant response to grazing.

6. *Synthesis and applications.* Intensive grazing can increase the forage value of grasslands by the creation of lawns dominated by tolerant species. However, results at the species level showed that some species that were avoided by grazers also increased, indicating a potential risk of a shift in composition of grazing lawns towards states of low forage value. This suggests that periodical resting of lawns could be a good management tool to favour palatable species, minimizing the risk of undesired shifts in composition.

Key-words: diet selection, fertile steppes, forage quality, grazing tolerance, leaf toughness, resource availability, specific leaf area

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Introduction

Sustained grazing often reduces the forage value of rangeland due to depletion of some species and their replacement by non-palatable species (Dyksterhuis 1949; Milton & Hoffman 1984; James, Landsberg & Morton 1999; Tobler, Cochard & Edwards 2003). However, in some rangelands wild or domestic herbivores promote the increase of more nutritious and palatable species compared with ungrazed situations. Thus, patches or even entire communities of high forage quality and short stature are formed (Bakker, Leeuw & van Wieren 1983; Cargill & Jefferies 1984; McNaughton 1984), sometimes involving large shifts in species composition (Coppock *et al.* 1983a, 1983b; Whicker & Detling 1988; Pucheta *et al.* 1998; Posse, Anchorena & Collantes 2000; Cingolani *et al.* 2003). Because of their high quality, the patches are selected by herbivores and become known as grazing lawns (Hunter 1962; Bakker, Leeuw & van Wieren 1983; McNaughton 1984; Cid & Brizuela 1998; Posse, Anchorena & Collantes 2000; Cingolani *et al.* 2002). A positive feedback between grazing intensity and forage quality results (Adler, Raff & Lauenroth 2001). Plants that suffer a high rate of herbivory and yet persist or increase under heavy grazing, as happens in grazing lawns, are defined as grazing tolerant (Rosenthal & Kotanen 1994; Briske 1996). This strategy of coping with grazing is distinct from grazing avoidance, one of the most commonly reported strategies in range management literature (Dyksterhuis 1949), which involves chemical or morphological traits that prevent plant consumption (Rosenthal & Kotanen 1994).

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Plant tolerance to herbivory involves both intrinsic and extrinsic factors (Rosenthal & Kotanen 1994). Among intrinsic factors, growth rate is one of the most important (Coley, Bryant & Chapin 1985; Herms & Matson 1992; Westoby 1999). Among extrinsic factors, the influence of resource availability to support regrowth has been highlighted (Coley, Bryant & Chapin 1985; Herms & Matson 1992; Hobbie 1992; Chapin 1993). To support high intrinsic growth rates, plants need to have high rates of resource capture from the environment, which are achieved by high capacities for photosynthesis and nutrient absorption per gram of tissue, which in turn require high nitrogen concentration in the leaves (Herms & Matson 1992; Chapin, Autumn & Pugnaire 1993). This characteristic generally increases leaf quality and selectivity by herbivores (Chapin 1993; Westoby 1999), thus generating the positive feedback between grazing and plant quality (McNaughton 1984; Hobbie 1992; Chapin 1993; Adler, Raff & Lauenroth 2001). Due to physiological trade-offs, plants with high growth rates are not efficient in conserving resources (Chapin 1993; Chapin, Autumn & Pugnaire 1993; Westoby *et al.* 2002), hence a tolerant response to grazing would be less common in systems with low availability of resources (but see Rosenthal & Kotanen 1994).

Some easily measured foliar traits, such as specific leaf area (SLA) and leaf toughness, are closely correlated with growth rate and foliar nutrient content across a large set of species for different floras (Lambers & Poorter 1992; Reich, Walters & Ellsworth 1992; Díaz *et al.* 1999; Reich *et al.* 1999; Pérez-Harguindeguy *et al.* 2000; Westoby *et al.* 2002). As these traits reflect fundamental growth–defence (or storage) trade-offs, plants that tolerate grazing should have high SLA and low leaf toughness. Plant height is another trait recognized as important in the plant response to grazing (Westoby 1999; Díaz, Noy-Meir & Cabido 2001). While some results suggest that a short stature could be a mechanism of grazing avoidance (Sala *et al.* 1986; Noy-Meir, Gutman & Kaplan 1989; Díaz-Barradas *et al.* 2001), others have documented the preference of herbivores for short lawns in relation to tall grasslands (Hunter 1962; Bakker, Leeuw & van Wieren 1983; McNaughton 1984). Accounting for this contradiction, Westoby (1999) suggested that the relationship between plant height and herbivore preference depends on the system under study. Some evidence suggests that in grassland systems with high resource availability, short species are favoured by grazing because they are more tolerant, and not because they escape grazing (Díaz, Noy-Meir & Cabido 2001).

In the fertile steppes of Tierra del Fuego, grazing reduces the abundance of the tall dominants, which are only moderately consumed by sheep, and promotes the increase of shorter grasses and forbs, many of them highly preferred (Posse, Anchorena & Collantes 1996, 2000). As a result, grazing lawns and open tussock grasslands have partially replaced the original closed tussock grasslands and shrublands (Cingolani 1999; Collantes, Anchorena & Cingolani 1999; Posse, Anchorena & Collantes 2000). Overall, short lawns have higher nutrient content and relative productivity (i.e. productivity per unit of biomass) than the dominant tussock community (Posse 1997; Anchorena *et al.* 2001) and support higher stocking rates (Cingolani, Anchorena & Collantes 1998; Posse, Anchorena & Collantes 2000; Cingolani *et al.* 2002). These studies, at community and landscape levels, suggest that grazing by non-native herbivores leads to the replacement of grazing-susceptible species by grazing-tolerant species. However, so far no comparisons among species' responses have been performed to test this hypothesis.

In this study we investigated the tolerance response of plants to grazing by analysing three components of the grazing–forage quality feedback, plant traits, herbivore selectivity and plant response to grazing, in the fertile steppes of Tierra del Fuego (southern Patagonia, Argentina). The relationships between them were analysed at two different levels, species and community. At the first level we predicted that species with a positive response to grazing (i.e. grazing increasers) would be selected by sheep, and would have higher SLA, lower stature and lower leaf toughness than those with a negative response to grazing. At the community

level, we predicted that sites with higher grazing intensities would have, on average, higher SLA and abundance of preferred plant species, and lower toughness and stature, compared with sites with lower grazing intensity.

Materials and methods

STUDY AREA

The study was carried out on the Mar?a Behety ranch and its surroundings (c. 60 000 ha), located near R?o Grande city (53°47'S, 67°42'W), Tierra del Fuego province, Argentina. It is at the centre of the Fuegian Magellanic steppe, a more humid variant of the Patagonian Magellanic steppe (Le?n *et al.* 1998). Mean annual rainfall is 363 mm, evenly distributed throughout the year. The climate is cloudy, cold and windy, with mean temperatures of 10°C in summer and 0°C in winter, when snow is common (Anchorena *et al.* 2001). Soil varies between landscape types, producing a soil fertility gradient to which vegetation responds. There is a gradual shift from dwarf shrub heaths (with *Empetrum rubrum* Vahl ex Willd as the dominant species) in meltwater plains with very infertile soils, to *Festuca gracillima* Hooker f. grasslands and *Chiliodichum diffusum* (Forster f) O. Kunze shrublands in tertiary landscapes with fertile soils (Collantes, Anchorena & Cingolani 1999). Our study focused on the fertile part of the gradient, where 100 years of domestic grazing have induced a decrease of tussocks and shrubs concomitant with an increase of short grasses and forbs, most of them native (Cingolani 1999; Collantes, Anchorena & Cingolani 1999; Posse, Anchorena & Collantes 2000). As in the rest of Patagonia, the vegetation has been exposed for a long time to grazing by wild populations of guanaco *Lama guanicoe* Muller; Camelidae (Lauenroth 1998; Adler *et al.* 2004). However, there is evidence that the density of sheep in the first decades after their introduction in Patagonia was considerably higher than native grazers (Golluscio, Deregibus & Paruelo 1998). Fire, either natural or human induced for pasture management, is uncommon in the area.

FLORISTIC DATA

Floristic composition was sampled at 34 sites (17 site pairs) on both sides of fence lines with contrasting physiognomies, indicating differences in the domestic grazing pressure experienced since the construction of the fences approximately 80 years ago (Cingolani 1999). We used a point-line method (Levy & Madden 1933), recording all vascular species in three lines of 50 points at intervals of 20 cm. The percentage cover value for a species was the average of the three lines. Species that were observed close to the lines but not touched with the needle were registered, and a cover value of 0.3% was arbitrarily assigned to them (i.e. less than 0.67%, the minimum cover that could be estimated

with the lines). Relative grazing intensity on both sides of the fence lines was assessed through historical information, present stocking rates, information from ranch administrators, proximity to sites preferred by sheep (e.g. warmer north-facing slopes; Anchorena *et al.* 2001), field evidence of disturbance and dung deposition (Cingolani 1999). Thus, for every fence line each side was classified as more intensively grazed or less intensively grazed.

SPECIES RESPONSE TO GRAZING

For each species (*s*), we calculated a grazing response index (*GRI*; modified from Noy-Meir & Oron 2001) in the following way:

$$GRI_s = \frac{\sum_{i=1}^n \frac{SGsi - SLsi}{SGsi + SLsi}}{n} \quad \text{eqn 1}$$

Where *SGsi* is the total cover of species *s* in the more intensively grazed side of pair *i*, *SLsi* the total cover of species *s* in the less grazed side of the same pair (*i*) and *n* the number of pairs where the species is present on at least one side. The *GRI* index varies between -1 (species that are present only on the less grazed sides of the fences) and +1 (species that are present only on the more intensively grazed sides of fences). Intermediate values represent the magnitude of decrease or increase with grazing, with values close to zero indicating the lack of a consistent response of the species to grazing. We calculated *GRI* only for the 35 species for which we had diet information (see below), all of which were present in at least four site pairs.

SPECIES SELECTIVITY

Proportions in sheep diets of the 35 most common species (dominants, subdominants and frequent subordinates) were obtained in a previous study (Posse, Anchorena & Collantes 1996). The microhistological technique (Holechek, Vavra & Pieper 1983) was used to determine diet composition in two non-contiguous paddocks. For each paddock, three to seven fresh composite faecal samples were collected throughout the paddock, in the four seasons. The faecal sample slides were prepared according to Williams (1969), and five slides were analysed for each sample at 100× magnification. On each slide, 20 microscope fields were observed. The presence or absence of each diet item was registered and the relative percentage was calculated. The proportional cover of each species in the available vegetation was estimated using a detailed map of the paddocks (Cingolani, Anchorena & Collantes 1998), from 20 to 22 floristic samples distributed in all map units of each paddock. From the proportion in the diet and the proportion in the field we calculated for each species and each paddock the Ivlev (1961) electivity index as:

$$EI = (D_s - V_s)/(D_s + V_s) \quad \text{eqn 2}$$

D_s and V_s are the proportions of species s in the diet and in the vegetation, respectively. This index also varies between -1 (maximum avoidance) and $+1$ (maximum selectivity). A value of zero indicates indifference, i.e. consumption in the same proportion as availability in the field. Although the abundance of species was different among paddocks, the selectivity values obtained were very similar. To calculate a single index for each species, we averaged the values from both paddocks. Only data from spring and summer were considered, because selectivity reaches its maximum expression in those seasons (Posse, Anchorena & Collantes 1996).

PLANT TRAITS

We measured SLA, leaf toughness and height for each of the 35 species, following protocols described in Cornelissen *et al.* (2003). To calculate SLA (leaf area divided by dry weight, $\text{mm}^2 \text{mg}^{-1}$), at least six fully expanded leaves per individual, for at least six individuals, were scanned and their areas calculated using scanner and image-analysis software. Dry weight was determined for the same leaves. Leaf toughness (leaf tensile strength, N mm^{-1}) was measured on at least 36 leaves from at least six individuals per species using a portable apparatus described in Hendry & Grime (1993). Plant height was measured from the base to the tip of the highest leaf (including the flag leaf in grasses) on at least 10 individuals. The three parameters were determined for each individual and then averaged per species.

DATA ANALYSIS

At the species level we calculated Pearson correlations among plant traits (SLA, leaf toughness and height), sheep selectivity (EI) and grazing response (GRI) across the 35 species together, and for monocotyledons and dicotyledons separately ($n = 18$ and $n = 17$, respectively). Height was log-transformed for this, and the following analyses at the species level, because it was skewed towards large values.

Additionally, to test for combined effects of variables, non-linear relations, and interactions, we performed two multiple regressions. In the first, we analysed the combined effects of plant traits on sheep selectivity. Sheep selectivity index was the dependent variable, and the three plant traits (SLA, leaf toughness and height) were the independent variables. In the second regression, we analysed the combined effects of plant traits and sheep selectivity on response to grazing. In this case, the GRI was the dependent variable, and plant traits together with sheep selectivity index the independent ones. In both cases, quadratic and interaction terms were included. Variables were selected through backward stepwise regressions. For both analyses, once relevant variables and terms were selected, we tested if the taxonomic difference among monocotyledons and dicotyledons could override the effects of the selected

variables or improve the variance explained. This was achieved by comparing sheep selectivity and GRI among monocotyledons and dicotyledons with ANOVA, including the selected variables as covariates.

To analyse the response to grazing at the community level, we calculated, for each of the 34 sites, a mean value for each plant trait and for sheep selectivity. This was performed by averaging the values of the component species in the site, weighed by their cover percentages. In this case, height was not transformed because the variable was normalized when averaged for site. We calculated Pearson correlations between the four variables across the 34 sites. We also performed paired comparisons (paired t -test) for each one of these variables, between the more grazed and the less grazed sides of the pairs ($n = 17$ pairs).

Results

SPECIES LEVEL

Over the whole set of species ($n = 35$) there were significant tendencies for taller plants to have lower SLA values and greater leaf toughness compared with shorter plants (Table 1). These correlations were maintained or strengthened within monocotyledons, but within dicotyledons height was not correlated with leaf toughness. Monocotyledons had tougher leaves than dicotyledons (t -test, $P < 0.05$), although there was no significant difference in SLA or height between the two groups.

Within dicotyledons, there was a significant tendency for sheep to select short plants and plants with tougher leaves, compared with tall plants and plants with soft leaves. These tendencies were not significant within monocotyledons, and either non-significant or marginally significant over the whole set of species (Table 2). SLA was not correlated with sheep selectivity in any set of species. These patterns were further explored through multiple regression of plant traits on sheep selectivity (Table 3 and Fig. 1). This analysis showed that the relation between leaf toughness and sheep selectivity was quadratic. Sheep selectivity increased with increasing toughness until $c. 5 \text{ N mm}^{-1}$, but between 5 and 8 N mm^{-1} sheep selectivity reached a maximum

Table 1. Pearson correlation coefficients among plant traits for the whole set of species, and for dicotyledons and monocotyledons separately

		Log height	SLA
SLA	All	-0.42^*	–
	Dicotyledons	-0.49^*	–
	Monocotyledons	-0.45^\dagger	
Toughness	All	0.38^*	-0.34^*
	Dicotyledons	-0.15 NS	-0.47^\dagger
	Monocotyledons	0.73^{***}	-0.62^{**}

NS $P > 0.1$, $^\dagger P < 0.1$, $^* P < 0.05$, $^{**} P < 0.01$, $^{***} P < 0.001$.

Table 2. Pearson correlations of sheep selectivity with plant traits for the whole set of species, and for dicotyledons and monocotyledons separately

	All species	Dicotyledons	Monocotyledons
SLA	-0.02 NS	-0.13 NS	0.00 NS
Toughness	0.28†	0.57*	-0.18 NS
Log height	-0.22 NS	-0.52*	-0.26 NS

NS $P > 0.1$, † $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 3. Stepwise multiple regression results of plant traits on sheep selectivity ($R^2 = 0.59$). Regression coefficients and P -values are indicated

Variable	Coefficient	P
Toughness	0.578	< 0.001
Toughness ²	-0.045	< 0.001
Log height	-0.506	0.005
Constant	-0.550	0.012

and then decreased with toughness (Fig. 1a). As the negative part of the relation appeared to be determined by the tussock grass *Festuca gracillima*, we tested whether the quadratic regression model was maintained when eliminating this species. Similar coefficients and P -values of the variables were obtained, with $R^2 = 0.56$, while a linear model still produced a clearly lower determination coefficient ($R^2 = 0.45$). The multiple regression also showed that sheep selectivity decreased with height, coinciding with trends found with simple correlations (Table 2 and Fig. 1b). Interaction terms were not significant. The difference in sheep selectivity between monocotyledons and dicotyledons was not significant when including the variables selected by the regression analysis as covariates.

Species grazing response showed significant correlations with SLA and plant height, but not with sheep selectivity and leaf toughness (Table 4). Small species with high SLA tended to increase with grazing, while

Table 4. Pearson correlations of the GRI with plant traits and sheep selectivity for the whole set of species, and for dicotyledons and monocotyledons separately

	All species	Monocotyledons	Dicotyledons
Selectivity	0.17 NS	-0.18 NS	0.08 NS
SLA	0.39*	0.19 NS	0.54*
Toughness	-0.05 NS	-0.39 NS	0.11 NS
Log height	-0.38*	-0.40†	-0.56*

NS $P > 0.1$, † $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

tall species with low SLA tended to decrease. These tendencies were strong for dicotyledons and very weak for monocotyledons. The multiple regression analysis did not improve the understanding of these relations. The regression model selected only SLA, with low explained variance (15.4%). A similarly low value (14.6%) was obtained when the regression was performed with height as the independent variable (Fig. 2). When both variables were forced together in the model, the explained variance increased to 21%, but neither variable was significant ($P = 0.11$ and $P = 0.13$ for SLA and height, respectively). When testing differences in GRI among monocotyledons and dicotyledons, including SLA (the variable selected by the regression analysis) as covariate, differences were not significant.

RESPONSE AT THE WHOLE COMMUNITY LEVEL

For 34 sampling sites, the mean sheep selectivity of the community (the weighted average of species selectivity indices) was strongly and negatively correlated with mean height, and positively correlated with mean SLA (Table 5). SLA and height were negatively correlated with each other. Leaf toughness was not significantly correlated with any variable. Paired comparisons among the more grazed and the less grazed sides of the fence lines showed that more intense grazing induced a significant reduction in community height, an increase

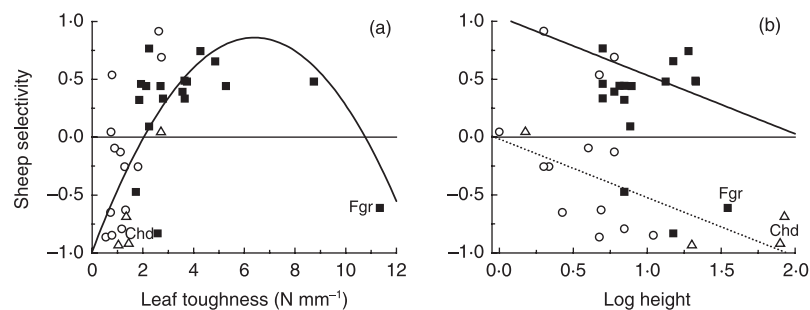
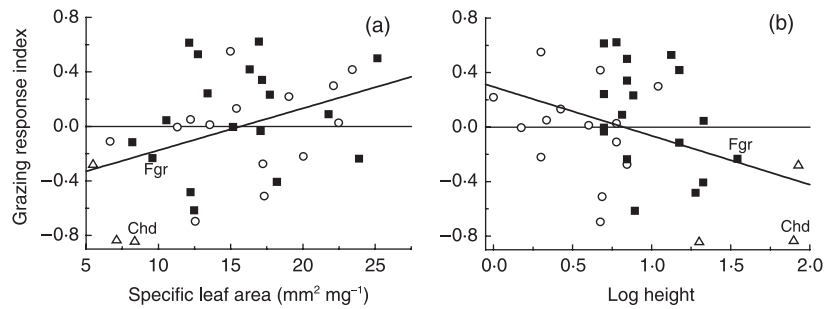


Fig. 1. Scatterplots of leaf toughness and plant height against sheep selectivity for monocotyledon (squares), herbaceous dicotyledon (circles) and woody dicotyledon (triangles) species. The curves represent the best-fit functions obtained for the whole data set, according to the multiple regression model in Table 3. In (a), the curve was plotted considering a constant value for log of plant height = 0.87 (the mean value in our data set, equivalent to 7.4 cm). In (b) lines represent the functions for leaves with low (dotted lines) and intermediate (continuous lines) toughness values, which were fixed arbitrarily at 1 and 4 $N\ mm^{-1}$, respectively. In both figures, dominants are indicated: Fgr, *Festuca gracillima*; Chd, *Chilotrichum diffusum*.



3 Fig. 2. Scatterplots of SLA (a) and height (b) against GRI for monocotyledon (squares), herbaceous dicotyledon (circles) and shrubby dicotyledon (triangles) species. Lines represent the best-fit functions of the whole data set for each variable: (a) $GRI = -0.483 + 0.031 \times SLA$ ($R^2 = 0.154$, $P < 0.05$); (b) $GRI = 0.295 - 0.359 \times \log \text{ height}$ ($R^2 = 0.146$, $P < 0.05$). In both figures, dominants are indicated: Fgr, *Festuca gracillima*; Chd, *Chiliotrichum diffusum*.

Table 5. Correlation between plant traits averaged per sampling site, across all the 34 sites

	Selectivity	Height	SLA
Height	-0.78***		
SLA	0.66***	-0.87***	
Toughness	0.14 NS	0.12 NS	-0.14 NS

NS $P > 0.1$, † $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 6. Paired comparisons (paired *t*-test) between the most grazed side of the pair and the less grazed side

	Mean difference (more grazed – less grazed)	<i>P</i>
Height (cm)	-8.80	0.000
SLA ($\text{mm}^2 \text{mg}^{-1}$)	1.96	0.000
Toughness (N mm^{-1})	-0.27	0.501
Selectivity index	0.164	0.001

in SLA and an increase in the abundance of species selected by sheep, but no change in average leaf toughness (Table 6).

Discussion

SPECIES LEVEL

Shorter species had leaves with higher SLA and/or lower toughness, a similar pattern to that found in other areas (Díaz *et al.* 1999; Lavorel & McIntyre 1999; Díaz, Noy-Meir & Cabido 2001). These results suggest that short plants have higher quality and growth rate, and are more tolerant to herbivory than taller plants. A trade-off between support and growth could explain these relationships. Taller plants have competitive advantages through prior access to light, but their investment in support tissues is costly. Shorter plants, in turn, could maximize growth by minimizing costs related to support (Westoby *et al.* 2002). Additionally, the low SLA and/or high toughness could be a way of coping with the harsh climatic conditions (wind, frosts) to which taller plants are more exposed in the Patagonian

steppe. The presence of some relatively tall woody species with low SLA but soft leaves (*Empetrum rubrum* and *Chiliotrichum diffusum*) weakened the correlations among toughness and the other traits. When calculated for dicotyledons alone, the height–toughness correlation was not significant, while for monocotyledons, needing to have structural strength in their leaves to reach higher stature, the correlation was significant.

As predicted, sheep selected shorter plants over taller ones, indicating that a short stature is not an effective avoidance strategy in relation to sheep, the small mouth and body size of which allow them to eat very close to the ground (Schwartz & Ellis 1981; Hanley 1982; Hodgson *et al.* 1991). The avoidance of taller plants is probably not related to their height *per se*; rather, it seems to be caused by the associated low quality of their leaves. For example, *Festuca gracillima*, which forms a tussock of about 30 cm of height, has lower quality (estimated through nitrogen concentration) than the shorter, non-tussock sward (Posse 1997; Anchorena *et al.* 2001; Mendoza *et al.* 2002). The three tallest shrubs (*Berberis buxifolia* Lam., *Chiliotrichum* and *Empetrum*), all with low SLA, are able to grow successfully in poor environments (Collantes, Anchorena & Cingolani 1999), suggesting that they have low intrinsic growth rates and nutrient content in their leaves (Berendse & Elberse 1990; Chapin, Autumn & Pugnaire 1993).

However, direct plant quality indicators (SLA and leaf toughness) were not related to sheep selectivity as expected. SLA was not related at all, and leaf toughness showed a unimodal response. Selectivity by invertebrate herbivores has been found to be negatively related to leaf toughness and positively related to SLA and other direct indicators of high quality (Coley 1983; Herms & Matson 1992; Cornelissen *et al.* 1999; Díaz *et al.* 1999; Pérez-Harguindeguy *et al.* 2003). As leaf toughness is positively associated with fibre content (Coley 1983), plants with hard leaves have low digestibility and are less preferred. Nevertheless, in this study sheep appeared to respond negatively to toughness only beyond a threshold level. This was the case for the tussock grass *Festuca gracillima*, similar to other tussock grasses elsewhere that are generally avoided due to their

very low digestibility (Hunter 1962; Bakker & Ruyter 1981; Bakker, Leeuw & van Wieren 1983; INTA 1997; Golluscio *et al.* 1998). Excluding *Festuca gracillima*, the relation between toughness and selectivity was still quadratic, but mostly positive. This result is unusual and surprising. The selection of tougher plants by sheep could be partially explained by higher amounts of chemical defences in the softer leaves of the perennial dicotyledons of this flora compared with the tougher leaves of grasses (Schwartz & Ellis 1981; Coughenour 1985). A similar inverse relation among leaf toughness and chemical defences could be present within dicotyledons in our study area. Some of the dicotyledons with softer leaves are known to have high concentrations of chemical defences, for instance *Empetrum rubrum* (Moore & Williams 1970), *Chilotrimum diffusum* (K. Braun, personal communication), *Rumex acetosella* L. and *Oxalis enneaphylla* Cav. (Moore 1983). It is also possible that the proportion of species with soft leaves in the diet (and hence their selectivity) was underestimated due to the use of microhistological technique to estimate the diet composition (Holechek, Vavra & Pieper 1983).

Contrary to our expectations, response to grazing did not show any relationship with sheep selectivity. The response of each species was related only with two plant traits, SLA and height. Although tall species are not highly selected by sheep, they are consumed in winter when regrowth is impossible (Posse, Anchorena & Collantes 1996). Additionally, trampling contributes to their mechanical destruction (Cingolani 1999; Anchorena *et al.* 2001; Stoffella 2003). Their low SLA values suggest that a low recovery capacity after damage (low tolerance) is the cause of their decrease, even with moderate grazing intensity. These results were opposite to those obtained by Anderson & Briske (1995), who found that selective herbivory of dominants (or late seral species), rather than a lesser expression of herbivore tolerance, was the main mechanism contributing to herbivore-induced species replacement in mesic grasslands. In our case, short species with high SLA could have benefit from grazing through the elimination of light competition from taller but slower-growing species (Westoby *et al.* 2002). Compensatory growth also operates (McNaughton 1983). Similar trends in the response to grazing of SLA and height were found by Díaz, Noy-Meir & Cabido (2001) on mesic grasslands in Argentina and Israel, but the opposite was found by Wardle, Bonner & Barker (2002) in New Zealand *Nothofagus* forests, where browsing clearly favours low-quality species. In contrast, Vesik, Leishmann & Westoby (2004) did not find a consistent response of height and SLA to grazing for semi-arid Australian rangelands. The low R^2 for the GRI suggests that there are other factors involved in the grazing response not accounted for here. Additionally, the relationships of grazing response with plant traits and sheep selectivity could be obscured because, in many cases, species do not have a consistent increaser or decreaser response,

but rather the response depends on the grazing context (Noy-Meir, Gutman & Kaplan 1989; Westoby, Walker & Noy-Meir 1989; Westoby 1999; Vesik & Westoby 2001).

COMMUNITY LEVEL

At the whole community level, the patterns were closer to our expectations. Shorter swards with higher than average SLA supported species that were preferred by sheep compared with taller swards with lower SLA. Additionally, short swards have experienced a greater grazing pressure during the history of domestic grazing in the area. Previous studies have shown that sheep select grazing lawns or more open tussock grasslands over closed tussock grassland and shrublands (Posse, Anchorena & Collantes 2000; Anchorena *et al.* 2001; Cingolani *et al.* 2002). The differences between the results obtained at the species and community levels are related to the characteristics of the dominants. Under ungrazed and lightly grazed situations the dominants are *Chilotrimum* and *Festuca*, two avoided but highly susceptible tall species with low SLA (Oliva 1996; Stoffella 2003). Grazing produces a partial replacement of these dominants by several subordinate species, increasing evenness and the average selectivity index, even when many of the replacement species are still avoided (Cingolani 1999; Collantes, Anchorena & Cingolani 1999; Posse, Anchorena & Collantes 2000). These replacement species are functionally different from previous dominants, as judged by their SLA and height values. This fact determined an overall decrease in height and increase in SLA with increasing grazing. As SLA is related to key ecosystem processes, such as litter decomposition and productivity (Cornelissen *et al.* 1999; Pérez-Harguindeguy *et al.* 2000; Lavorel & Garnier 2002), grazing in this case markedly changed ecosystem functioning. This change in the functional properties of the community is in contrast with the predictions of Walker, Kinzig & Langridge (1999), who suggested that, due to functional redundancy in ecosystems, disturbance would produce a replacement of dominant species by subordinates with similar functional properties, without strong changes in ecosystem functioning.

CONCLUSION

The results at the community level support the hypothesis that in environments with high resource availability, tolerance is the most successful strategy to cope with grazing. The greater tolerance of some subordinate species, compared with the lesser tolerance of dominants, seems to be the main mechanism driving grazing-induced species replacement. However, at the species level more complex patterns appeared. The lack of relationship between sheep selectivity and grazing response indicates that not all increaser species are tolerant. On the contrary, many species having traits that apparently

indicate a high quality (i.e. high SLA and/or low toughness) are in fact avoided. Chemical defences could be playing a more important role in this area than expected, allowing some short species to achieve high growth rates without incurring the cost of being eaten, and to increase within the grazing lawn community under grazing.

The results obtained in this study have practical implications for range management in the humid Magellanic steppe and similar rangelands. In general, the grazing-induced formation and maintenance of short, productive and palatable grazing lawns at the expense of tall, tough grassland has been considered to favour animal nutrition and production (McNaughton 1984). It has been implicitly assumed that in these cases intensive grazing can only improve animal production and no special care in management is necessary. The results here indicate the potential risk of a shift in composition of grazing lawns towards a dominance of species avoided by sheep. This study highlights the importance of studying in more detail the variation within lawns and possible effects of management once the lawn is formed. In the study area, tussocks hardly return after grazing has eliminated them (Cingolani 1999). Thus, there are potential management tools, such as periodical rests, for improving lawn composition and forage value, which would not favour tussocks but could benefit palatable short species.

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