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PRIORITY CONTRIBUTION

Can grazing response of herbaceous plants be predicted from simple vegetative traits?

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Summary

1. Range management is based on the response of plant species and communities to grazing intensity. The identification of easily measured plant functional traits that consistently predict grazing response in a wide spectrum of rangelands would be a major advance.

2. Sets of species from temperate subhumid upland grasslands of Argentina and Israel, grazed by cattle, were analysed to find out whether: (i) plants with contrasting grazing responses differed in terms of easily measured vegetative and life-history traits; (ii) their grazing response could be predicted from those traits; (iii) these patterns differed between the two countries. Leaf mass, area, specific area (SLA) and toughness were measured on 83 Argentine and 19 Israeli species. Species were classified by grazing response (grazing-susceptible or grazing-resistant) and plant height (< or > 40 cm) as well as by life history (annual or perennial) and taxonomy (monocotyledon or dicotyledon).

3. Similar plant traits were associated with a specific response to grazing in both Argentina and Israel. Grazing-resistant species were shorter in height, and had smaller, more tender, leaves, with higher SLA than grazing-susceptible species. Grazing resistance was associated with both avoidance traits (small height and leaf size) and tolerance traits (high SLA). Leaf toughness did not contribute to grazing resistance and may be related to selection for canopy dominance.

4. Plant height was the best single predictor of grazing response, followed by leaf mass. The best prediction of species grazing response was achieved by combining plant height, life history and leaf mass. SLA was a comparatively poor predictor of grazing response.

5. The ranges of plant traits, and some correlation patterns between them, differed markedly between species sets from Argentina and Israel. However, the significant relationships between plant traits and grazing response were maintained.

6. The results of this exploratory study suggest that prediction of grazing responses on the basis of easily measured plant traits is feasible and consistent between similar grazing systems in different regions. The results challenge the precept that intense cattle grazing necessarily favours species with tough, unpalatable, leaves.

Key-words: Argentina, comparative studies, Israel, leaf traits, specific leaf area.

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Introduction

Land use and management actions on plant communities induce responses and changes in the community. These vegetation responses, in turn, modify the economic and other benefits that can be obtained from the managed system. The explanation and prediction of plant community responses to land use and management factors is therefore a major objective in applied as well as theoretical ecology. The basic unit for which the response is usually observed is at the population or species level. However, results from studies of particular communities, if they consist simply of species lists with their associated responses, cannot be generalized or compared beyond the limits of the local situation. Comparison and integration of community responses observed in floristically distinct regions, and extrapolation to predict plant responses in new situations, require a transformation to a level more general than the species. In regions with a rich and imperfectly known flora, the species level may be problematic even for primary observations of responses. Therefore, there is a growing need to understand and predict plant responses to different land management factors in terms of plant traits that are easily measured and at the same time ecologically meaningful (Díaz & Cabido 1997; Lavorel *et al.* 1997; Westoby 1998; Hodgson *et al.* 1999; Weiher *et al.* 1999).

Grazing by domestic herbivores has both extensive and profound impacts on plant communities. Vegetation changes in response to grazing management decisions often modify primary plant and animal production and economic returns from the system, as well as other benefits like conservation value. The identification of plant types and traits that explain and predict the response of species and communities to grazing intensity is one of the main tools in management of grazing systems. Almost a century of empirical research in rangelands in different parts of the world has been dedicated to identifying the response of individual plant species to varying grazing intensities. For some ecosystems, in particular North American grasslands, the results from many studies have led to the formulation of generalizations on the plant types or plant traits associated with a negative or a positive response to grazing intensity (grazing decreasers or grazing increasers and invaders, respectively; Dyksterhuis 1949; Ellison 1960).

Generalizations across communities and continents on plant traits that can explain, or predict, responses of plant species to grazing intensity can be derived by theoretical considerations (Milchunas, Sala & Lauenroth 1988; Westoby 1999) and evaluated by comparing or integrating information from communities in different regions. The comparative approach requires measurement and recording of a common set of traits in different species, together with independent information on species responses to grazing. Recently, attention has focused on identifying a minimum set of the most important plant traits that must be considered in relation to grazing response (Landsberg, Lavorel & Stol 1999; Weiher *et al.* 1999; Westoby 1999).

Decreases in plant height and leaf size in response to grazing by ungulates have been repeatedly documented in the literature (Sala *et al.* 1986; McNaughton & Sabuni 1988; Noy-Meir, Gutman & Kaplan 1989; Díaz, Acosta & Cabido 1992; Landsberg, Lavorel & Stol 1999). Leaf toughness or resistance to tearing has been associated with low palatability and grazing avoidance (Coley, Bryant & Chapin 1985; Herms & Matson 1992; Grime *et al.* 1996; Cornelissen *et al.* 1999). In the last few years, the importance of specific leaf area as a trait that integrates plant investment into growth vs. defence and storage, and its value as an easily measured indicator of relative growth rate, have been highlighted by several authors (Garnier 1992; Lambers & Poorter 1992; Reich, Walters & Ellsworth 1992; Westoby 1998; Hodgson *et al.* 1999). Recently, Westoby (1999) has proposed a scheme in which specific leaf area and plant height play a major role in response to disturbance, in particular to grazing. According to his model, plants with high specific leaf area should be favoured under conditions of heavy, non-selective, grazing, whereas plants with low specific leaf area should predominate when stocking rate is moderate or low, thus allowing grazers to feed selectively.

Within this context, we analysed species sets from temperate, subhumid, upland grasslands of central Argentina and northern Israel in order to answer the following questions.

1. Do plants with contrasting responses to grazing differ in terms of easily measured traits, such as plant height, life history, leaf area, leaf mass, specific leaf area or leaf tensile strength?

2. What is the trait or combination of traits among those measured that can better explain and predict the grazing response of species in this set?

3. Are the answers to the first two questions similar in sets of species from two different floras, and in the combined species set?

Methods

STUDY SITES

The Argentine study area was the upland grasslands of Sierras Grandes (Córdoba Mountains, central Argentina), developed mostly on granitic substrate at altitudes ranging from 1400 to > 2200 m a.s.l., with an annual rainfall ranging from *c.* 840 to *c.* 912 mm and an annual mean temperature ranging from *c.* 12 to *c.* 8 °C. The climate is temperate subhumid with a monsoonal rainfall distribution (Acosta *et al.* 1989). According to Díaz, Acosta & Cabido (1994) and Díaz *et al.* (1999), the region has a relatively long history of grazing by native (mostly Camelidae) and domestic ungulates, with moderate to high stocking rates of livestock of European origin during the last 400 years. At present the area is grazed by cattle and to a lesser degree by horses and sheep. Plant community composition and species responses to grazing have been studied extensively by Acosta *et al.* (1989), Cabido, Acosta & Díaz (1989), Díaz, Acosta & Cabido (1992, 1994), Pucheta, Díaz & Cabido (1992) and Pucheta *et al.* (1998).

The Israeli study site was Mediterranean subhumid grassland on stony basaltic soil near Almagor on the Korazim Plateau in Galilee, at an altitude of 100 m a.s.l. (300 m above the Sea of Galilee) The mean annual rainfall is *c.* 500 mm (Almagor rainfall station) and the mean annual temperature is 21 °C (Anonymous 1995). The region has a very long history of intense grazing by domestic herbivores (Noy-Meir & Seligman 1979; Perevolotsky & Seligman 1998). Domestic goats and sheep have been documented in this region from about 8500 BP and domestic cattle before 7000 BP (Smith 1995). At present, most of the area is grazed by cattle at moderate to high intensities. The responses to grazing of the plant community and of many individual species is fairly well known from previous studies (Noy-Meir, Gutman & Kaplan 1989; Noy-Meir 1995; Noy-Meir & Sternberg 1999).

SPECIES SET

The Argentine species set included 83 native species for which information was available on both response to grazing and on basic plant and leaf traits. This set is a fairly representative sample of the entire herbaceous flora of the area and includes most of the common species. Exotic species in the area are mostly associated with agricultural plots and road verges. In grazed sites, they represent an extremely low proportion of total vegetation cover and species richness, and do not change significantly under different grazing intensities (Díaz, Acosta & Cabido 1994). Therefore, they were not considered in this study. The Israeli species set consisted of 19 common species of known grazing response, from which leaf trait measurements could be obtained in April 1999. The Israeli sample represented the main functional types and grazing responses encountered in the flora, although not necessarily in exact proportion to their relative frequencies. The combined Argentine–Israeli species set thus consisted of 102 species.

TRAIT MEASUREMENTS

Measurements of leaf traits for each species were taken from a sample of at least 24 fully expanded, but not senescing, healthy leaves from at least six sexually mature individuals. Mean area per leaf (leaf area in mm^2) was measured on the fresh leaves by scanning five to eight samples of three to five leaves at a time and estimating their area in the image with a scanner and the software Optimetrics® (Bioscan, Edmonds, USA). Mean dry mass per leaf (leaf mass in mg) was estimated by oven-drying until a constant weight (60 °C) and then weighing the same leaf samples. From these two measurements, mean specific leaf area (SLA) was calculated ($\mathrm{mm}^2\ \mathrm{mg}^{-1}$). Leaf tensile strength, or resistance to tearing, was measured with a tensile-strength meter constructed on the basis of Hendry & Grime (1993), and expressed as force needed per unit of width of a leaf sample ($\mathrm{N\ mm}^{-1}$). Plant height was expressed as a categorical variable, with species classified into low (< 40 cm maximum foliage elevation) or tall (> 40 cm). Life history, i.e. annual vs. perennial, was determined on the basis of the regional floras. Taxonomic affiliation of the species was defined at the highest level, as monocotyledons vs. dicotyledons.

GRAZING RESPONSE

On the basis of previous studies (Acosta *et al.* 1989; Cabido, Acosta & Díaz 1989; Noy-Meir, Gutman & Kaplan 1989; Díaz, Acosta & Cabido 1992, 1994; Pucheta, Díaz & Cabido 1992; Pucheta *et al.* 1998; Noy-Meir & Sternberg 1999), species were initially divided into three categories. Grazing decreasers or grazing-susceptible species (G–) were consistently more abundant in ungrazed or lightly grazed sites than in moderately to heavily grazed sites (> 25% consumption of above-ground net primary productivity). Grazing increasers (G+) were species that consistently showed the opposite trend. The third group (G0) included species that did not respond consistently to grazing intensity and those that had maximum abundance at some intermediate grazing intensity. The G0 group on its own was too small for statistical inference and was therefore combined with G+ into one grazing-resistant group (G0+). It should be noted that grazing response as evaluated here includes both direct and indirect (community-mediated) effects of grazing on a species. For example, a G+ species may benefit from the reduced competition and increased light availability in grazed sites, rather than from growth stimulation by grazing. The proportion of G– and G0+ plants was not significantly different between the Argentine and the Israeli species sets ($P = 0{\cdot}30$ by Fisher's exact test). A complete list of species and grazing responses is given in the Appendix.

STATISTICAL ANALYSIS

Three types of statistical analysis were carried out, in order to answer different questions. First, to examine trait differences between species with different responses to grazing, grazing response (categorical) was defined as the independent variable, while each of the other species traits in turn was the dependent variable. For continuous traits (leaf mass, leaf tensile strength and SLA), the differences between grazing response groups in the values of the trait, transformed to natural logarithms (ln) to normalize distribution and to equalize variances, were evaluated by the *t*-test and simple analysis of variance. Significance of the difference is presented as P, the probability of a value of t or F, respectively, being greater than the observed value. The proportion of variance explained (r^2) is evaluated as the ratio of sum of squares in the model (grazing response) to total sum of squares. Means for continuous traits are presented without the transformation, to facilitate biological interpretation. For categorical traits (life history, height, taxonomic affiliation and country), the significance of difference in traits frequencies between grazing response groups was evaluated by Fisher's exact test for 2 × 2 contingency tables. A measure of the proportion of variance explained (R^2) in this case is the ratio of negative log-likelihoods (U) in the logistic regression of the categorical trait on grazing response (Sall, Lehman & Saul 1996). The analyses were carried out for Argentine ($n = 83$) and Israeli ($n = 19$) species sets separately and for the combined ($n = 102$) species set.

A second type of statistical analysis was designed to examine relationships between different traits that may affect the interpretation of the relationships of each of those traits with grazing response. In particular, the relationships of SLA (as dependent variable) with other traits were examined in detail, because SLA has been proposed as an integrated or diagnostic trait in the definition of plant functional types. Relationships between pairs of continuous traits were evaluated by linear correlation and regression of ln-transformed values, for the separate country sets and the combined data set. Relationships between a continuous (in particular SLA) and a categorical variable were analysed by t-test and by analysis of variance of ln-transformed values. In some cases, the joint effects of a categorical and a continuous variable (covariate) on another continuous variable (SLA) were analysed by general linear model ANOVA.

In the third type of statistical analysis, grazing response (G–/G0+) was defined as the dependent variable to be predicted, and both continuous and categorical species traits were defined as the independent variables or potential predictors. Because grazing response is a binary categorical variable, only the probability of a species being G– or G0+ can be predicted, and the appropriate statistical model is logistic regression. Analyses with single species traits and with combinations of two or more traits were carried out in search of the 'best' model for prediction of grazing response, i.e. the model with the highest R^2 (the ratio of negative log-likelihoods U). These analyses were in general carried out only with the combined data set, but in some cases the separate country sets were analysed to clarify specific points.

Results

TRAIT DIFFERENCES BETWEEN SPECIES WITH DIFFERENT RESPONSES TO GRAZING

Continuous traits

In the combined data set, all four continuous traits were significantly different between grazing response groups, i.e. between G– and G0+ species (Table 1). In decreasing order of variance of the trait accounted for by grazing response, G– species had larger leaves (by mass, then by area) and stronger leaves than G0+ species. G0+ species had on average higher SLA, but this difference accounted for only 4% of the variance in SLA and was not as highly significant as for the other traits. The trends described for the combined data set for the four traits in relation to grazing response were qualitatively maintained in the separate data sets for both Argentina and Israel (Table 1).

For all continuous traits, there were highly ($P < 0{\cdot}001$) significant differences between the species sets from the two countries (Table 2, top). Plants in the Israeli set had on average higher leaf mass, higher leaf area and higher SLA, but lower leaf tensile strength, compared with Argentine plants. Despite these large differences,

Table 1. Mean values of continuous traits for grazing-resistant (G0+) and grazing-susceptible (G–) species response groups in the combined Argentine–Israeli data set ($n = 102$ species) and in the separate Argentine ($n = 83$) and Israeli ($n = 19$) sets. Means are of untransformed data. P is the significance of the difference in ln-transformed trait values between grazing response groups, by ANOVA. r^2 is the adjusted proportion of variance accounted for by grazing response in the same analysis. The traits are ranked by r^2 in the combined data set. Significantly ($P < 0{\cdot}05$) higher values for each trait are presented in bold

Trait	Mean G0+	Mean G–	r^2	P
Combined data set				
Leaf mass (mg)	26·9	**108·4**	0·200	**< 0·001**
Leaf area (mm^2)	411	**1363**	0·125	**< 0·001**
Leaf tensile strength (N mm^{-1})	2·49	**8·67**	0·098	**< 0·001**
Specific leaf area (mm^2 mg^{-1})	**16·1**	12·6	0·044	**0·012**
Argentina				
Leaf mass (mg)	18·6	**74·0**	0·191	**< 0·001**
Leaf area (mm^2)	188	**587**	0·129	**< 0·001**
Leaf tensile strength (N mm^{-1})	2·78	**10·71**	0·158	**< 0·001**
Specific leaf area (mm^2 mg^{-1})	**13·9**	10·9	0·063	**0·012**
Israel				
Leaf mass (mg)	87·5	**217·4**	0·244	**0·018**
Leaf area (mm^2)	1506	**3818**	0·167	**0·047**
Leaf tensile strength (N mm^{-1})	1·05	2·20	0·013	0·282
Specific leaf area (mm^2 mg^{-1})	**27·0**	18·1	0·350	**0·004**

Table 2. Means of leaf traits, and the differences between means of these traits in grazing-resistant (G0+) and grazing-susceptible (G–) species response groups (both in ln-transformed values). Both means and grazing response differences are presented for the combined species set and the separate country sets. The last column shows the differences between Argentine and Israeli species sets in the ln-transformed means and grazing response differences. Bold type indicates differences that are significantly different from zero ($P < 0·05$, *t*-test)

Traits	Combined	Argentina	Israel	Difference Argentina–Israel
Means of ln (variable)				
Leaf mass (mg)	2·49	2·19	3·83	**–1·64**
Leaf area (mm^2)	5·05	4·61	6·98	**–2·37**
Leaf tensile strength (N mm^{-1})	0·71	0·90	–0·14	**+1·04**
Specific leaf area (mm^2 mg^{-1})	2·56	2·43	3·14	**–0·71**
Differences ln (variable) between G0+ and G–				
Leaf mass (mg)	**–1·72**	**–1·61**	**–1·65**	+0·04
Leaf area (mm^2)	**–1·40**	**–1·24**	**–1·26**	+0·02
Leaf tensile strength (N mm^{-1})	**–0·86**	**–1·06**	–0·54	–0·52
Specific leaf area (mm^2 mg^{-1})	**+0·32**	**+0·37**	**+0·39**	–0·02

the 'grazing effect', defined as the mean difference in traits (measured on a ln-scale) between grazing response groups, was remarkably similar in the two countries (Table 2, bottom). In the cases of leaf mass and leaf area, the grazing effect in the combined data set was as great or greater than in both separate country data sets (Table 2, bottom). The mixing of two data sets representing different floras with different ranges of these traits did not mask the relationship between trait and grazing response but rather strengthened it. For SLA, the grazing effect in the combined data set was slightly smaller than for both separate data sets, that is some masking occurred by the combination for this trait. For leaf tensile strength, the grazing effect on the combined data set was intermediate between the effects observed in separate country sets.

Categorical traits

The categorical trait that showed the strongest association with grazing response in the combined data set was plant height: 76% of G– species were tall (> 40 cm) vs. only 13% tall species among G0+ species ($P < 0·001$ by Fisher's exact test for 2 × 2 contingency tables). Also significant was the difference in the representation of monocotyledons and dicotyledons in the grazing response groups: 72% of G– plants were monocotyledons, compared with only 35% monocotyledons in G0+ plants ($P = 0·001$). The proportion of perennials (vs. annuals) was somewhat greater in the G– group than in the G0+ group, but this difference was not significant in the combined species set (G– 80% perennials, G0+ 69%, $P = 0·21$) or in the Argentine set alone (G0– 95%, G+ 83%, $P = 0·28$). Perennials represented 86% of the Argentine species set and only 11% of the Israeli set.

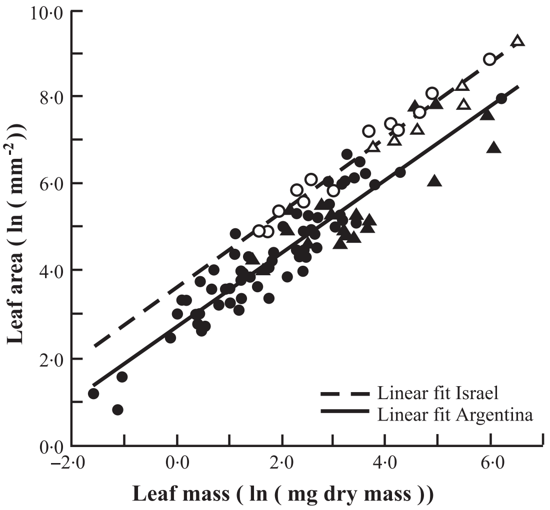

Fig. 1. The relationship between leaf area and leaf dry mass, both transformed to natural logarithms, over all species in the data set. Separate regression lines for 83 Argentine species (solid symbols) and 19 Israeli species (empty symbols). Triangles = grazing-susceptible species (G–); circles = grazing-resistant species (G0+).

RELATIONSHIPS BETWEEN SLA AND OTHER VARIABLES

There were significant relationships between traits that must be taken into account in the interpretation of the relationships between traits and response to grazing. Most obviously, leaf area and leaf mass were strongly and significantly associated, considering both the whole database and individual countries (Fig. 1). The regression lines for the two countries had almost equal slopes, but the intercept was significantly higher for Israeli plants (3·64 ± 0·33, 95% confidence interval) than for Argentine plants (2·74 ± 0·20). Israeli species showed consistently larger leaf area per unit leaf mass (mean SLA = 24·2) than Argentine species (mean SLA = 12·7, difference significant at $P < 0·001$).

In the combined data set, annuals had significantly higher SLA (mean = 21·8) than perennials (mean = 12·7, $R^2 = 0·24$, $P < 0·001$). A similar but weaker trend was also found in the Argentine set alone (annuals 17·1 vs. perennials 12·6, $R^2 = 0·062$, $P = 0·013$). In the Israeli data set, all but two species were annuals, which

Table 3. Univariate relationships between SLA (as dependent variable) and each one of the other leaf traits in the combined species set and in the separate country sets, by regression with ln-transformations of all variables. Parameters presented are the slope parameter (b) of regression, the significance (P) of the slope being different from zero, and the proportion of variance accounted for by regression (R^2). Traits are ranked by R^2 in the combined data set. Significant ($P < 0·05$) regressions are presented in bold

	Combined			Argentina			Israel		
Independent variable	Slope	R^2	P	Slope	R^2	P	Slope	R^2	P
Leaf tensile strength	**–0·305**	0·332	**< 0·001**	**–0·293**	0·305	**< 0·001**	–0·001	0·000	0·916
Leaf area	**+0·080**	0·039	**0·026**	–0·003	0·000	0·939	**– 0·113**	0·195	**0·033**
Leaf mass	–0·053	0·011	0·147	**–0·146**	0·138	**< 0·001**	**–0·130**	0·370	**0·003**

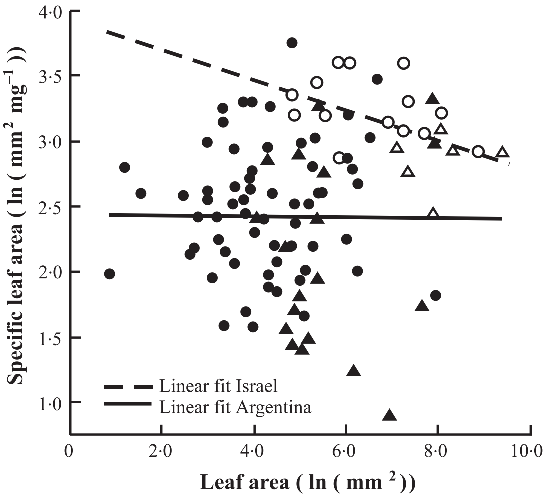

Fig. 2. The relationship between specific leaf area and leaf area, both transformed to natural logarithms, over all species in the data set. Separate regression lines for 83 Argentine species (solid symbols) and 19 Israeli species (empty symbols). Triangles = grazing-susceptible species (G–); circles =grazing-resistant species (G0+).

explains in part the higher mean SLA in this country. However, Israeli annuals also had significantly greater SLA than Argentine annuals (R^2 = 0·33, n = 27, P < 0·001). Thus, the combination of country and life-history factors explained a somewhat larger proportion of variance in SLA (R^2 = 0·27) than either life history (R^2 = 0·24) or country (R^2 = 0·21) alone. Dicotyledons had significantly higher SLA (17·2) than monocotyledons (12·8), but this explained only 8% of the variance in SLA in the combined data set (R^2 = 0·08, P = 0·002). In the Argentine data set, low plants had on average somewhat higher SLA (14·0) than tall plants (9·7; P = 0·001), but in the combined data set there was no significant relationship between SLA and plant height.

SLA was significantly and strongly negatively correlated with leaf tensile strength in the Argentine and in the combined sample of species (Table 3). In other words, leaves with high SLA tended to be weaker, as might be expected from mechanical considerations. This factor alone accounted for 33% of the variance of SLA in the combined data set, considerably more than life history (24%) or country (21%). An additive bifactorial model including highly significant (P < 0·001) effects of both life history (annuals > perennial) and leaf tensile strength (negative) predicted as much as 43% of variation in SLA among species.

Some unexpected effects were observed in the statistical correlations between SLA and the two variables of which it is the ratio, leaf area and leaf mass. In the sample of Israeli species, SLA was negatively correlated not only with leaf mass (which might be expected if only from a pure algebraic consideration) but also with leaf area (P = 0·033), i.e. larger leaves also tended to have more mass per unit area. In the Argentine sample there was no correlation between leaf area and SLA, with rather large and independent variations of both variables. All combinations, large and high SLA, large and low SLA, small and high SLA, and small and low SLA leaves, were common (Fig. 2). When samples from both countries were combined, a new pattern appeared that was different from those observed in the separate samples (Table 3). In the combined data set, SLA showed a weak but significant positive correlation with leaf area, while the negative correlation between SLA and leaf mass disappeared. Inspection of the scatter of species in the SLA vs. leaf area graph showed that the Israeli species extended the circular cloud of Argentine species into a region of larger leaves with higher SLA (Fig. 2), hence the positive correlation in the combined set.

BEST PREDICTORS OF PLANT RESPONSE TO GRAZING

When species response to grazing (– vs. 0+) was selected as the dependent (predicted) variable, the best single predictor of this response, in the combined set of species, was plant height as categorical variable (Table 4). Only 8% of low or medium height (< 40 cm) species were G–, compared with 66% of species taller than 40 cm.

The second best single predictor of grazing response was leaf mass: larger leaves tended to be associated with a negative response to grazing. A similar association with leaf area was significant but with a lower determination coefficient. Additional significant single predictors of decreasing effectiveness were leaf tensile strength (stronger leaves, G– species) and

Table 4. Best logistic regression models for prediction of the probability of grazing response of a species (– or 0+) from other traits, in the combined data set ($n = 102$), allowing both continuous and categorical predictors to be included in the models. All one-variable models are presented, ranked by the proportion of variance explained by the model R^2. Only significant two-variable models are presented, ranked by R^2. The 'effect' for categorical variables is a trait state and the associated grazing response; for continuous variables, + (or –) means that higher values of the variable predict a higher probability of + (or –) grazing responses. Significance (P) levels of the effects are denoted as follows: NS ($P > 0{\cdot}05$), *($P < 0{\cdot}05$), **($P < 0{\cdot}01$), ***($P < 0{\cdot}001$)

	One-variable models		
	Variable 1		
R^2	Trait	Effect	P
0·306	Height	Low +	***
0·203	Leaf mass	–	***
0·124	Leaf area	–	***
0·097	Leaf strength	–	**
0·093	Dicot/monocot	Dicots +	**
0·048	SLA	+	*
0·011	Life history		NS
0·005	Country		NS

	Two-variable models					
	Variable 1			Variable 2		
R^2	Trait	Effect	P	Trait	Effect	P
0·401	Height	Low +	***	Life history	Annuals +	**
0·369	Height	Low +	***	Dicot/monocot	Dicots +	*
0·361	Height	Low +	***	Leaf strength	–	*
0·349	Leaf mass	–	***	Leaf strength	–	***
0·347	Leaf area	–	***	Leaf strength	–	***

Table 5. Association between grazing response and life history, in different plant height categories. Each cell contains the number of species with each grazing response within the given life history, as absolute number and as percentage of the total number of species with this life history. The significance of association (lack of independence) is given by Fisher's exact test for 2 × 2 contingency tables

		Grazing response class		
Height class	Life history	G–	G0+	P (Fisher)
Tall plants ($n = 29$)	Annuals	4 (30%)	9 (69%)	
	Perennials	15 (94%)	1 (6%)	**0·001**
Low plants ($n = 73$)	Annuals	1 (6%)	15 (94%)	
	Perennials	5 (9%)	52 (91%)	0·607
All plants ($n = 102$)	Annuals	5 (17%)	24 (83%)	
	Perennials	20 (27%)	53 (73%)	0·320

taxonomic affiliation (dicotyledons were more G0+). SLA, although marginally significantly associated with grazing response (higher SLA with G0+ species), was the continuous variable with the smallest predictive value (Table 4).

Life history alone was not a significant predictor of grazing response in the combined data set, although a somewhat greater proportion of annuals (83%) than of perennials (73%) was classified as having a positive or neutral response to grazing (G0+; Tables 4 and 5). However, when life history was added as a second factor to height, it increased considerably the predictive power of the model, resulting in the best two-factor model for predicting response to grazing (Table 4). This was because, among tall plants, the proportion of G0+ plants was significantly greater in annuals than in perennials (69% vs. 6%; Table 5). Among low plants there was no such significant difference between life histories, because almost all the low plants are G0+. Because there are more low than tall plants in the data set, the life-history effect found among tall plants gets swamped by the low plants and the life-history effect alone is not significant in the whole data set (Table 5). When the height effect is already in the model, the life-history effect (expressed among tall plants) significantly improves the prediction of grazing response (Table 4). Although the data indicated an interactive effect of height and life history on grazing response, the additional interaction term was not quite significant ($P = 0{\cdot}056$).

When height was excluded from the model to predict grazing response, a good prediction could also be obtained by a two-factor model combining leaf tensile strength with leaf mass or leaf area (Table 4). SLA did not significantly contribute to any two-factor model. The best prediction of whether a species in our database responded negatively to grazing or not, was achieved by combining plant height, life history and leaf mass. In this three-factor model all effects were significant and it slightly improved the determination coefficient (0·44) compared with the two-factor model with height and life history only (0·40).

Discussion

Similar plant trait responses were associated with grazing by livestock in Argentina and Israel. In general, species that showed a positive or neutral response to grazing tended to have shorter height and smaller, more tender, leaves, with higher SLA compared with species that showed a negative response to grazing. Short plant height and small leaves are typical mechanisms of grazing resistance by grazing avoidance (*sensu* Briske 1996, 1999) that have been documented in many other studies (Sala *et al.* 1986; McNaughton & Sabuni 1988; Noy-Meir, Gutman & Kaplan 1989; Díaz, Acosta & Cabido 1992; Landsberg, Lavorel & Stol 1999). However, another common mechanism of grazing avoidance, leaf toughness (and low SLA), that is usually associated with low palatability (Coughenour 1985; Grime *et al.* 1996; Cornelissen *et al.* 1999) did not contribute to grazing resistance in this species set. On the contrary, grazing resistance was associated with tender leaves and (weakly) with high SLA, as predicted by Westoby (1999) for heavily grazed areas, suggesting higher growth rate as a mechanism of grazing tolerance (*sensu* Briske 1996, 1999).

The trends reported here for Argentine and Israeli grasslands match the predictions of the models of McNaughton (1984) and Milchunas, Sala & Lauenroth (1988) for subhumid grasslands with a long evolutionary history of grazing: intense grazing favours short plants with high regrowth rates, rather than tough, unpalatable plants. High growth rates tend to be negatively correlated with quantitative defences, such as leaf toughness (Herms & Mattson 1992). These results contradict a classical precept of range management, that palatability in grassland communities responds inversely to grazing intensity (Ellison 1960). Although the latter phenomenon has often been observed in some regions of the world (North America, Ellison 1960; South Africa, Morris, Tainton & Hardy 1992), the present results support the view that response to grazing is more diverse and depends on the evolutionary and climatic context of grazing in different regions (Perevolotsky & Seligman 1998). For example, grasslands in Argentina, presumably with a similar evolutionary history of grazing, and under relatively similar management regimes, differ in their responses to grazing. Responses similar to the ones described in this article have been found for some moderately to heavily grazed subhumid grasslands (Posse, Anchorena & Collantes 1996, 2000). On the other hand, opposite trends have been reported for semi-arid grasslands, in which continuous grazing is often associated with tough and unpalatable plant species (Distel & Boó 1996). This might be related to lower resource availability or lower grazing intensity. According to general models, grazing avoidance should be favoured against grazing tolerance in situations of water or nutrient scarcity (Herms & Mattson 1992; Hobbie 1992). According to Westoby (1999), lower grazing intensity in a short growing season may allow more effective avoidance of tough leaves by grazers.

G– species in productive Argentine and Israeli grassland grazed by cattle tended to be tall, with large, tough, leaves. This suggests that leaf toughness, rather than serving to deter grazers, is related to the advantages of having stiff, erect, leaves to search for light in the closed canopy that develops in the absence of grazing. In Argentina, large leaves with low SLA are mostly fibrous leaves of tall perennial tussock grasses (‘chocolate-box’ leaves; *sensu* Grubb 1986; Cunningham, Summerhayes & Westoby 1999), whereas in Israel species with large leaves and low SLA are broad-leafed annual dicotyledons, with tender lamina and strong thick veins (‘kite’ structure; *sensu* Grubb 1986; Cunningham, Summerhayes & Westoby 1999).

In general, Argentine species showed lower SLA and higher leaf tensile strength than Israeli species. This higher degree of sclerophylly does not seem to be associated with nutritional or water-balance deficiencies. Although Córdoba montane grasslands receive considerably more precipitation than Galilee grasslands, seasonality (rainfall strongly concentrated to the warm season) determines a much higher evapotranspiration rate, and therefore the moisture regime can be considered roughly similar. Above-ground net primary productivity is similar (around 300 g m^{-2} $year^{-1}$ in both cases; Seligman & Gutman 1979; Pucheta *et al.* 1998), and N and P availability is not as low as to be commonly limiting in the soil of either system. It may be speculated that the higher occurrence of sclerophylly in the flora of these Argentine mesic grasslands is linked with their historically less intense grazing regime, and therefore stronger selection for canopy dominance, compared with the eastern Mediterranean (Milchunas, Sala & Lauenroth 1988; Perevolotsky & Seligman 1998; Díaz *et al.* 1999).

From a practical point of view, the best single predictor of response to grazing in our joint data set was plant height, followed by leaf mass. The best prediction of whether a species in our database responded negatively to grazing or not, was achieved by combining plant height, life history and leaf mass. Despite the suggestion of its key role in understanding plant trait responses to grazing (Díaz & Cabido 1997; Westoby 1999), SLA showed a poor predictive value of grazing response. Within the context of our data set, plant height and leaf mass appeared as better predictors of grazing response than SLA. They are also considerably easier to measure, as SLA has some operational complications (Weiher *et al.* 1999; Wilson, Thompson & Hodgson 1999).

The ranges of plant height, leaf size, leaf strength and SLA differed markedly between the species samples from the two countries. The patterns of correlation between some of these structural traits were also different between countries. However, the significant relationships between these plant traits and grazing response were maintained and in some cases strengthened by combining the Argentine and Israeli species sets. This exploratory study allows cautious optimism regarding the prospects of generalizing relationships between simple plant traits and grazing responses across continents, in communities and grazing systems that share similarities in productivity, grazing history and present grazing management. In particular, the results indicate that intense cattle grazing in productive natural grasslands with a long history of grazing will result mainly in an increase of short species with small tender leaves, at the expense of tall species with large tough leaves. Animal intake and productivity in the intensely grazed rangeland will therefore be limited by small bite size, but not necessarily by low palatability or low primary productivity.

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Appendix

Species included in the data set and their response to grazing by domestic ungulates. G– = grazing-susceptible; G0+ = grazing-resistant (see text for definition and further details). Nomenclature follows Zuloaga *et al.* (1994) and Zuloaga & Morrone (1996, 1999) for Argentine species, and Zohary & Feinbrun-Dothan (1966–86) for Israeli species

Species	Family	Grazing response
Argentina		
Acicarpha tribuloides	Calyceraceae	G0+
Adesmia bicolor	Fabaceae	G0+
Agrostis montevidensis	Poaceae	G0+
Alternanthera pumila	Amaranthaceae	G0+
Astragalus parodii	Fabaceae	G0+
Bidens andicola var. *decomposita*	Asteraceae	G0+
Bothriochloa laguroides	Poaceae	G0+
Briza subaristata	Poaceae	G0+
Bromus auleticus	Poaceae	G–
Bromus catharticus	Poaceae	G–
Bulbostylis juncoides	Cyperaceae	G0+
Cardionema ramosissima	Caryophyllaceae	G0+
Carex fuscula	Cyperaceae	G0+
Cerastium arvense	Caryophyllaceae	G0+
Chaptalia integerrima	Asteraceae	G0+
Chevreulia sarmentosa	Asteraceae	G0+
Chloris retusa	Poaceae	G0+
Cologania ovalifolia	Fabaceae	G–
Cotula mexicana	Asteraceae	G0+
Cuphea glutinosa	Lythraceae	G0+
Cyperus reflexus	Cyperaceae	G–
Deyeuxia hieronymi	Poaceae	G–
Dichondra repens var. *holosericea*	Convolvulaceae	G0+
Eleocharis albibracteata	Cyperaceae	G0+
Eragrostis lugens	Poaceae	G0+
Eryngium agavifolium	Apiaceae	G0+
Eryngium nudicaule	Apiaceae	G0+
Euphorbia serpens	Euphorbiaceae	G0+
Festuca hieronymi	Poaceae	G–
Festuca tucumanica	Poaceae	G–
Galactia marginalis	Fabaceae	G0+
Gamochaeta filaginea	Asteraceae	G0+
Gentianella parviflora	Gentianaceae	G0+
Glandularia dissecta	Verbenaceae	G0+
Gnaphalium gaudichaudianum	Asteraceae	G0+
Hieracium giganteum var. *setulosum*	Asteraceae	G–
Hypochaeris argentina	Asteraceae	G–
Hypoxis humilis	Hypoxidaceaae	G–
Juncus achalensis	Juncaceae	G0+
Juncus uruguensis	Juncaceae	G0+
Lachemilla pinnata	Rosaceae	G0+
Lepidium bonariense	Brassicaceae	G0+
Melica macra	Poaceae	G–
Mitracarpus cuspidatum	Rubiaceae	G0+
Muhlenbergia peruviana	Poaceae	G0+
Nothoscordum inodorum	Liliaceae	G0+
Noticastrum marginatum	Asteraceae	G0+
Oenothera indecora	Onagraceae	G0+
Oxalis sexenata	Oxalidaceae	G0+
Paspalum notatum	Poaceae	G0+
Paspalum quadrifarium	Poaceae	G–
Pfaffia gnaphaloides	Amaranthaceae	G0+
Piptochaetium montevidense	Poaceae	G0+
Plantago australis	Plantaginaceae	G0+
Plantago brasiliensis	Plantaginaceae	G0+
Poa resinulosa	Poaceae	G0+
Poa stuckertii	Poaceae	G–
Pratia hederacea	Campanulaceae	G0+
Relbunium richardianum	Rubiaceae	G0+
Rhynchosia senna	Fabaceae	G0+
Rumex acetosella	Polygonaceae	G0+

Appendix *Continued*

Species	Family	Grazing response
Schizachyrium microstachyum	Poaceae	G0+
Schizachyrium spicatum	Poaceae	G0+
Schkuhria pinnata	Asteraceae	G0+
Setaria parviflora	Poaceae	G0+
Sisyrinchium unguiculatum	Iridaceae	G0+
Sorghastrum pellitum	Poaceae	G–
Spergula ramosa	Caryophyllaceae	G0+
Sporobolus indicus	Poaceae	G0+
Stenandrium dulce	Acanthaceae	G0+
Stipa eriostachya	Poaceae	G–
Stipa filiculmis	Poaceae	G–
Stipa neesiana	Poaceae	G0+
Stipa tenuissima	Poaceae	G–
Stipa trichotoma	Poaceae	G–
Stylosanthes gracilis	Fabaceae	G0+
Tagetes argentina	Asteraceae	G0+
Taraxacum officinale	Asteraceae	G0+
Trifolium repens	Fabaceae	G0+
Tripogon spicatus	Poaceae	G0+
Vicia graminea	Fabaceae	G–
Vulpia myuros	Poaceae	G0+
Zephyranthes longistyla	Amaryllidaceae	G0+
Israel		
Avena sterilis	Poaceae	G0+
Psoralea bituminosa	Fabaceae	G–
Brassica nigra	Brassicaceae	G0+
Bromus alopecurus	Poaceae	G0+
Cephalaria joppensis	Dipsacaceae	G–
Hordeum bulbosum	Poaceae	G–
Hordeum spontaneum	Poaceae	G–
Linum pubescens	Linaceae	G0+
Medicago granadensis	Fabaceae	G0+
Phalaris paradoxa	Poaceae	G0+
Pimpinella cretica	Apiaceae	G0+
Raphanus rostratus	Brassicaceae	G0+
Rapistrum rugosum	Brassicaceae	G0+
Scabiosa prolifera	Dipsacaceae	G0+
Synelcosciadium carmeli	Apiaceae	G–
Trifolium nigrescens	Fabaceae	G0+
Trifolium pilulare	Fabaceae	G0+
Trifolium purpureum	Fabaceae	G0+
Triticum dicoccoides	Poaceae	G–