

Plant trait responses to grazing – a global synthesis

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Abstract

Herbivory by domestic and wild ungulates is a major driver of global vegetation dynamics. However, grazing is not considered in dynamic global vegetation models, or more generally in studies of the effects of environmental change on ecosystems at regional to global scale. An obstacle to this is a lack of empirical tests of several hypotheses linking plant traits with grazing. We, therefore, set out to test whether some widely recognized trait responses to grazing are consistent at the global level. We conducted a meta-analysis of plant trait responses to grazing, based on 197 studies from all major regions of the world, and using six major conceptual models of trait response to grazing as a framework. Data were available for seven plant traits: life history, canopy height, habit, architecture, growth form (forb, graminoid, herbaceous legume, woody), palatability, and geographic origin. Covariates were precipitation and evolutionary history of herbivory. Overall, grazing favoured annual over perennial plants, short plants over tall plants, prostrate over erect plants, and stoloniferous and rosette architecture over tussock architecture. There was no consistent effect of grazing on growth form. Some response patterns were modified by particular combinations of precipitation and history of herbivory. Climatic and historical contexts are therefore essential for understanding plant trait responses to grazing. Our study identifies some key traits to be incorporated into plant functional classifications for the explicit consideration of grazing into global vegetation models used in global change research. Importantly, our results suggest that plant functional type classifications and response rules need to be specific to regions with different climate and herbivory history.

Keywords: dynamic global vegetation models, functional traits, global plant functional types, grazing history, grazing models, ungulate herbivores

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Introduction

Grazing by domestic and wild ungulates is the most globally widespread land use (FAOSTAT data 2004, <http://faostat.fao.org/>). After fire, grazing is the most

important disturbance of vegetation in terms of both area and biomass loss (Huntly, 1991). Grazing is both dependent on (e.g. Day & Detling, 1990; Huntly, 1991) and affects (e.g. Briske, 1996) plant morphological and functional traits. This codependency can generate powerful feedback cycles between the structure and biochemistry of vegetation and the cycling and storage of nutrients (Huntly, 1991; Wardle & Bardgett, 2004). Effects include altered disturbance regimes, especially fire (e.g. Scholes & Archer, 1997; Bachelet *et al.*, 2000; Bond *et al.*, 2003; Bond, 2005), and regional climate (Eastman *et al.*, 2001), and changes to above- and below-ground diversity (Landsberg *et al.*, 1999; Wardle & Bardgett, 2004). For these reasons, changes in grazer densities in response to climate and/or land use change are increasingly considered an important element of global change (Wardle & Bardgett, 2004).

Dynamic global vegetation models (DGVMs) seek to represent vegetation dynamics generically in order to project the effects of global environmental change on the distribution of vegetation types and on key biogeochemical cycles at continental scales (Cramer *et al.*, 2001). An important advance in achieving this has been the simplification of vegetation composition using plant functional groups (Lavorel *et al.*, 2007). However, successful selection of relevant plant functional groups, and representation of vegetation dynamics require identification of the key processes that drive species distribution. Initial developments of DGVMs focussed mainly on plant responses to climate and atmospheric CO₂ concentration, and have successfully captured the distribution of biomes and their contribution to the carbon cycle (Cramer *et al.*, 2001; Sitch *et al.*, 2003). Although recent models successfully include effects of land use change and agricultural land cover modification (McGuire *et al.*, 2001), the approach has been a 'static' one, which incorporates land cover effects, rather than the processes causing the change. The next generation of DGVMs needs to include dynamic simulations of fire and other disturbances (Bond *et al.*, 2003). There have been attempts to incorporate grazing in regional models of vegetation dynamics (Bachelet *et al.*, 2000; Daly *et al.*, 2000; Bond *et al.*, 2003), but grazing is not yet incorporated in DGVMs. A major obstacle to this is the lack of information about which plant traits are positively or negatively associated with grazing at the global scale (Díaz *et al.*, 2002; Skarpe, 2000).

There are thousands of published studies of plant responses to grazing. Those which use plant traits provide a more general and mechanistic basis for understanding plant behaviour (Díaz *et al.*, 2001; Lavorel & Garnier, 2002; see also Vesk & Westoby, 2001), but have generally focused on local conditions. As a result,

most current models of plant trait responses (see Briske, 1996 for review) are extrapolated from these local studies, and there are very few examples of comparisons of grazing effects between regions with contrasting climates and/or evolutionary histories of herbivory (Bock *et al.*, 1995; Adler *et al.*, 2004). Because of this, the validity of many hypothesized trait responses to grazing remains untested at the global level. None of the studies that focus on grazing from a global perspective (Milchunas *et al.*, 1988; Milchunas & Lauenroth, 1993; Briske, 1996; Landsberg *et al.*, 1999) have explicitly tested the generality of plant trait responses to grazing over a range of environments.

Current conceptual models of trait response to grazing provide a framework of our analysis of the global-level consistency of associations between plant attributes and responses to grazing. Of the models available, we restrict our framework to (1) those models that offer explicit predictions of plant trait responses to grazing; and (2) only those predictions that could be tested, at least partially, with the published data available. The conceptual models considered lead to predictions about specific plant trait responses to grazing. These predictions vary in the extent to which they reflect common knowledge among range managers and scientists. Our analyses enable some of the predictions (Table 1) to be tested objectively using a global dataset.

The first model of plant trait response to grazing is the range-succession model (Dyksterhuis, 1949; Arnold, 1955). The range-succession model predicts an increase in annual plant cover and a decrease of perennials with grazing, replacement of palatable plants by unpalatable ones, and replacement of tall and midheight grasses by short grasses, subshrubs, and perennial prostrate forbs. The range-succession model assumes that these patterns are universal and unaffected by differences in the characteristics of different regions.

In contrast, the generalized model of Milchunas *et al.* (1988) focuses on the idea that precipitation (proxy for productivity) and grazing history influence plant community response. This model assumes that aridity and grazing select the same plant attributes. In humid habitats, however, canopy competition and grazing select opposite attributes. As a result, changes promoted by grazing should be maximal in humid systems with a short history of grazing. With a long history of grazing, grazing response should be minimal in dry systems for some traits (e.g. life history), but maximum in humid systems for other traits (e.g. height, habit).

A third group of models are based on the idea of plant strategies (i.e. general adaptations to resource capture, use and release, and recognize disturbance, of which grazing is a particular case, within their context disturbance is simply removal of biomass) as

Table 1 Summary of plant attributes favoured by grazing according to six models (see text for description)

Models	Traits								
	Sources	Factors	Life history	Canopy height	Habit	Architecture	Growth form	Palatability	Origin
Generalized	Milchunas <i>et al.</i> (1988), Milchunas & Lauenroth (1993)	Climate, history	Annual, more marked in humid systems	Short, more marked in systems that are humid and with long grazing history	Prostrate, more marked in systems with long herbivory history, both humid and dry, most marked in humid systems with long history	Stoloniferous, more marked in systems with long herbivory history, both humid and dry, most marked in humid with long history	Graminoid	–	Exotics in systems with short herbivory history both humid and dry, but most marked in humid systems
Range-succession	Dyksterhuis (1949), Arnold (1955)	None	Annual	Short	Prostrate	Rosette, stoloniferous	Forb, woody	Low	–
CSR	Grime (1977, 1990, 2001)	Climate*	Annual, more marked in humid systems	Short, more marked in dry systems	Prostrate, more marked in dry systems	–	–	Low in dry systems, high in humid systems	–
LHS	Westoby (1998, 1999)	None	–	Short	–	–	–	–	–
Resource availability	Coley <i>et al.</i> (1985), Herms & Mattson (1992)	Climate*	–	–	–	–	–	Low in dry systems, high in humid systems	–
Physiological	Briske & Richards (1995), Briske (1996)	None	–	Short	Prostrate	Stoloniferous	–	Low in dry systems, high in humid systems	–

*These models do not explicitly deal with dry vs. humid climates. The equation of dry with unproductive and humid with productive is ours (see 'Methods').

Columns 3–8 refer to factors and traits that were explicitly considered by different models in their original formulation and for which we could gather enough information. For example, specific leaf area is a prominent trait in Grime's (1977, 1990, 2001) and Westoby's (1998, 1999) models, but we did not find enough case studied reporting it. The description of the predicted plant attributes refers to the *response to grazing*, rather than the abundance of that attribute under particular environmental conditions. For example, the prostrate habit may be predicted to become more abundant in response to grazing in humid systems with a long evolutionary history of herbivory, even though that habit may be generally more common in dry systems than in humid systems.

an important regulator of plant traits. The other major factor is stress, which limits biomass production. Prominent examples of this approach are the models of Grime (1977, 1990, 2001) and Westoby (1998, 1999). Grime's CSR model distinguishes three principal plant strategies: Competitor, Stress-tolerator and Ruderal. Grazing selects plants with a ruderal (short-lived, small-sized, fast-growing) strategy. However, in dry systems stress-tolerators (small, prostrate, perennial) are also favoured. Similarly, grazing should lead to shorter plants, especially in dry systems. Palatability should increase in response to grazing in humid systems (grazing tolerance, involving fast regrowth of high-quality tissue with very low structural defence), and should decrease in dry systems (grazing avoidance, involving slow-growing tissue, rich in structural defence).

Westoby's (1998) LHS (leaf-height-seed) model is based on similar considerations to Grime's CSR model, but includes only three traits, specific leaf area, canopy height and seed mass. Westoby (1999) adapted this model to grazing response by examining which plant attributes were favoured by different grazing intensities. According to this model, moderate, selective grazing favours unpalatable plants, whereas heavy, nonselective grazing favours palatable plants. Plant response to grazing is not explicitly influenced by climate or evolutionary history of grazing.

The resource availability (Coley *et al.*, 1985) and related models (e.g. growth-differentiation model, see Herms & Mattson, 1992 and references therein) include the interactive effects of productivity and herbivory, and are based on the trade-off between plant allocation to the production of new photosynthetic tissue and antiherbivore defence. Like Grime's CSR model, the resource availability model predicts that grazing will select an avoidance strategy in dry (less-productive) systems, and a tolerance strategy through increased growth in humid systems. Herms & Mattson (1992) suggest that the stronger the historical impact of grazing, the stronger the plant investment into grazing avoidance, but in general these models do not explicitly address the effects of evolutionary history of grazing.

Finally, it has been argued that predictions about trade-offs between tolerance and avoidance strategies could also be reached via detailed investigation of physiological mechanisms underlying plant response to grazing within a single system, with no need to consider the effects of climate or evolutionary history (Briske & Richards, 1995; Briske, 1996). We refer to this approach as the 'physiological' model.

The CSR and resource availability models distinguish between productive and unproductive systems without reference to the determinants of productivity (e.g. water

or nutrient availability). In this study, we draw from the generalized model, and treat dry systems as a special case of unproductive systems. We base this on evidence of the general convergence of plant attributes in floras where the proximate cause of low productivity is water or nutrient availability (Díaz *et al.*, 2004).

This paper presents a synthesis of 197 grazing studies from a wide range of biomes across all inhabited continents. In it, we compare world wide, a range of studies of plant trait responses to grazing, within a standard framework and using a common set of descriptors. The aim of this synthesis was to address the following questions:

1. Do plant traits that are commonly accepted as being associated with grazing, behave consistently as expected when examined at a global scale?
2. Are associations between plant traits and grazing dependent upon regional patterns of precipitation and/or evolutionary history of herbivory?
3. Are the most commonly used conceptual models of plant trait response to grazing supported at a global scale?
4. Is the incorporation of grazing into global or regional models of vegetation dynamics justified? If so, which plant traits should be used to enhance them?

Methods

Data sources

We compiled and analysed literature from: Africa, Australia and New Zealand, Central Asia, North America, the Eastern and Western Mediterranean region, Northern and Central Europe and South America. The studies described in this literature cover different biomes including grasslands, managed pastures, savannahs, shrublands, tundra deserts and several types of woodland (Table 2). In the analysis, and following Lavorel *et al.* (1997), we distinguished between plant traits (e.g. canopy height, habit) and their attributes (i.e. the categories of traits, such as tall, short, erect, prostrate, etc.). Our focus was on plant trait responses to grazing and so we did not consider the papers whose sole focus was changes in biogeochemical processes or those containing taxonomic composition information that could not readily be translated into individual plant attributes.

In our data collection, we distinguished between publications, studies, and observations. Publications presented results of one or more studies of the effects of grazing (including browsing) on species richness and/or plant attributes. Some publications provided only site information so that a study or observation

Table 2 Summary of primary sources included in the dataset

Evolutionary history of herbivory Precipitation category	Long (113; 673)		Short (45; 331)	
	Dry (58, 211)	Humid (89, 462)	Dry (27, 178)	Humid (23, 153)
Africa (21, 67)	14, 41	7, 26	–	–
Australasia (28, 292)	–	–	9, 147	19, 145
Central Asia (5, 28)	5, 28	–	–	–
Mediterranean region (30, 259)	10, 44	20, 215	–	–
North America (45, 100)	12, 38	13, 28	18, 31	2, 3
Northern and Central Europe (37, 137)	4, 14	31, 118	–	2, 5
South America (31, 121)	13, 46	18, 75	–	–

Figures indicate number of studies, observations in each category.

See 'Methods' and Appendix B for definitions of precipitation and grazing history categories.

could be supported by more than one publication. Each study was a dataset representing an independent investigation of the responses to certain traits within a certain context (e.g. a comparison between different grazing regimes at one site and/or along a certain time sequence). Each observation was an identified response (positive, neutral or negative) in species richness or abundance of an attribute to two levels of grazing. Individual publications provided one or more studies, each containing one or (generally) more observations. In total, our dataset contained 1004 observations, belonging to 197 studies, reported in 194 publications (Table 2, Appendix A). In order to standardize the information, we used a proforma that included an exhaustive list of ancillary and response variables (Appendix B).

Variables used as covariates in the comparison of trait response

Precipitation [as a proxy for aboveground net primary productivity (ANPP)] and evolutionary history of herbivory by ungulates have been considered variables of paramount importance in previous work (Milchunas *et al.*, 1988; Milchunas & Lauenroth, 1993; Díaz *et al.*, 2001). We used two categories of precipitation (dry/humid, following Köppen, 1918), and two categories of grazing history (long, short; Table 2). The different biomes were classified as having long or short evolutionary history of grazing by large mammals on the basis of the duration of occupation by wild and domestic ungulates and/or similar mammalian herbivores according to van der Hammen (1983) (Africa), Atkinson & Greenwood (1989) and Landsberg *et al.* (1999) (Australasia), Zimov *et al.* (1995) (Central Asia), Edelstein & Milevsky (1994) (Mediterranean region), Milchunas & Lauenroth (1993) (North America), Agustí & Antón (2002) (Europe) and Franklin (1982) and Borrero (1996) (South America).

Ideally, we would have used ANPP rather than precipitation as a covariate, but the latter is more readily available. Precipitation is well correlated with herbaceous ANPP up to 900–1000 mm yr⁻¹ (Lauenroth, 1979; Milchunas & Lauenroth, 1993). This relationship is weaker in more humid systems where low temperatures cause very low evapotranspiration. Only about 3.2% of the observations in our dataset were from systems that were, or were likely to be, both humid and unproductive (ANPP < 300 g m⁻² yr⁻¹). These cases were well spread among regions (although there was no case in Africa, Central Asia and the Mediterranean region) and so were unlikely to bias the results. Thus, we believe that using precipitation as a proxy for ANPP is justified for the purposes of our analyses. Obviously, we could not find examples of all possible combinations of grazing history and precipitation regime in every region. Because of the typically large scale of operation of these processes, most regions had only one level of grazing history, and many were characterized by a single precipitation category (Table 2). Other ancillary variables (see Appendix B) were reported in too few studies for statistical analysis.

Selection of plant traits and response variables

The selection of plant traits was based on the works of Weiher *et al.* (1999), and Díaz *et al.* (2001). The initial search comprised 20 morphological, anatomical and physiological traits, but only six of these produced enough observations for statistical analysis. These were: life history (annual, perennial), canopy height (short, tall), habit (erect, prostrate), architecture (leafy stem, rosette, stoloniferous, tussock), growth form (forb, graminoid, herbaceous legume, woody) and palatability (palatable, unpalatable). Palatability had sufficient cases for analysis only when various forms of unpalatability (tough vs. tender, nonpalatable vs. palatable, good vs. poor forage, toxic, prickly, etc.) were pooled

together in the same trait. Although not a physical plant trait, geographic origin (native vs. exotic) was also included because the spread of potentially invasive exotic plants into new habitats and its relationship to grazing is relevant for theoretical (Milchunas *et al.*, 1988; Stohlgren *et al.*, 1999) and practical (Mooney & Hobbs, 2000) reasons. Abundance data were available for all seven traits. Frequency, biomass, cover and density were all accepted forms of abundance. Species richness (the total number of species having a particular attribute) data were available for three traits (life history, growth form, origin).

Only ca. 35% of the observations contained quantitative measurements or significance tests, and they were very unevenly distributed among regions and combinations of precipitation and history of grazing. Therefore, in order to take full advantage of the literature, we included reports of responses with and without statistical testing, including qualitative reports of the direction of change. Once this dataset was compiled, we searched for changes in response to grazing in the abundance and species richness of plants bearing certain attributes. We made no attempt to separate direct (e.g. defoliation) and indirect effects (e.g. competitive release and other community-mediated mechanisms) of grazing on plants. Plant responses can vary considerably depending on grazing intensity (e.g. Naveh & Whittaker, 1979; Milchunas *et al.*, 1988; Westoby, 1989), but many authors simply describe differences between 'grazed' and 'ungrazed' situations, without defining whether grazing intensity was heavy or light. Therefore, in this study, we simply compared grazed vs. ungrazed situations. Where more than one grazing treatment was studied we used the most extreme ones (lightest vs. heaviest) for our analysis. When absolute values of abundance were recorded for a single attribute within a trait, then no information could be derived for the alternative attribute(s). When, on the other hand, the records were relative values more than one record could be derived and included in the dataset (e.g. annual increase and perennial decrease).

Statistical analysis

We carried out a meta-analysis in the sense of applying formal statistical methods to the *post-hoc* analysis of a large collection of results from individual studies (Gurevitch & Hedges, 1999). We used a vote-counting technique because few of the compiled studies were suitable for the calculation of effect size. We constructed multiple contingency tables considering, for each trait and response variable (abundance or species richness), the different attributes (rows) and directions of response (columns). Within the cells, we considered the

frequency of positive, neutral or negative responses to grazing of plants bearing each attribute. Precipitation category and history of grazing were used as covariates to control for their effects on the association of interest (between trait and direction of response). We also used regions as a covariate to control for their effects on the association of interest (between trait and direction of response). The results were not strongly driven by any particular region, as region effects were mainly explained by precipitation and history categories.

We analysed the multiple contingency tables using the Cochran–Mantel–Haenszel General Association (CMH) test and the Maximum Likelihood χ^2 (G^2)-statistic (Agresti, 2002) for the partial tables (for each herbivory history and precipitation category combination). The CMH test was run controlling for the effects of grazing history and precipitation category to determine whether different combinations of these factors influenced the association between attributes and *direction of response to grazing*.

Changes in species richness were reported less frequently than changes in abundance. Only in the cases of life history and origin did we find sufficient species richness data to run meaningful tests for at least one of the combinations of precipitation and history of grazing. Frequently, the total number of cases was acceptable, but their distribution into precipitation \times history categories was markedly uneven creating empty categories and preventing us from performing tests (Appendix C).

Results

All associations between the direction of response to grazing and plant traits were considered at the global scale and under the different combinations of precipitation and evolutionary history of grazing. These are presented as contingency tables in Appendix C. The most ecologically significant patterns are highlighted below.

Life history

For plant abundance, there was a significant global association between the direction of response to grazing and life history. Positive responses by annual plants to grazing, and negative responses by perennial plants, were reported more frequently than other responses under all combinations of precipitation and herbivory history (Fig. 1a). The exception to this was dry systems with a long evolutionary history of herbivory (e.g. Mediterranean semiarid grasslands, American short-grass steppe, some African systems), in which no significant pattern was detected (Fig. 1b).

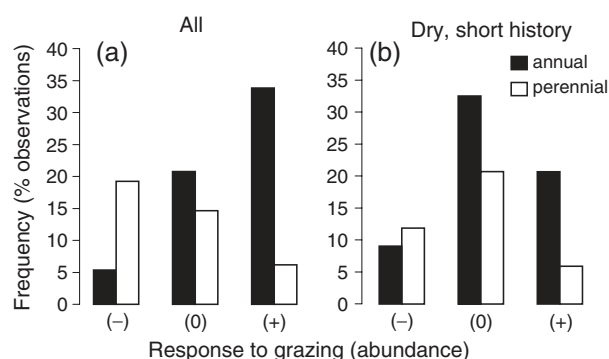


Fig. 1 Relative frequency of observations in which the abundance of annual and perennial plants decreased (-), did not change (0) or increased (+) with grazing. (a) Considering all sites, and controlling for the effects of precipitation (dry or humid) and evolutionary history of grazing (short or long); $P < 0.0001$, $n = 130$; Cochran-Mantel-Haenszel Association test. (b) In dry systems with long evolutionary history of grazing; $P = 0.353$, $n = 34$; G^2 -test.

The species richness of annuals and perennials was responsive to grazing across all sites, with observations of annuals increasing and perennials decreasing with grazing being the most frequent (Fig. 2a). Positive responses of annuals to grazing were more marked in humid systems but, within this precipitation category, the response seemed to depend on evolutionary history of herbivory. In humid systems with a short history of grazing, positive responses of annual plants to grazing and negative responses of perennial plants, were reported most frequently (Fig. 2b). In contrast, in humid systems with a long history, the pattern of responses of species richness to grazing did not differ significantly between annual and perennial plants (Fig. 2c). In the case of dry sites, there were insufficient data in either category of grazing history to calculate the G^2 -statistic (Appendix C).

Canopy height

Globally there was a significant association between the direction of response to grazing and plant height. Positive responses of short plants and negative responses of tall plants were reported most frequently in all systems (Fig. 3a), except in dry systems with a short evolutionary history (e.g. some Australian sites), where response to grazing did not differ significantly between short and tall plants (Fig. 3b). The general trend of positive response of short plants and negative response of tall plants was more marked in systems with a long history of grazing than in those with a short history (Fig. 3c and d). The trends observed in dry and humid systems were similar in direction and magnitude.

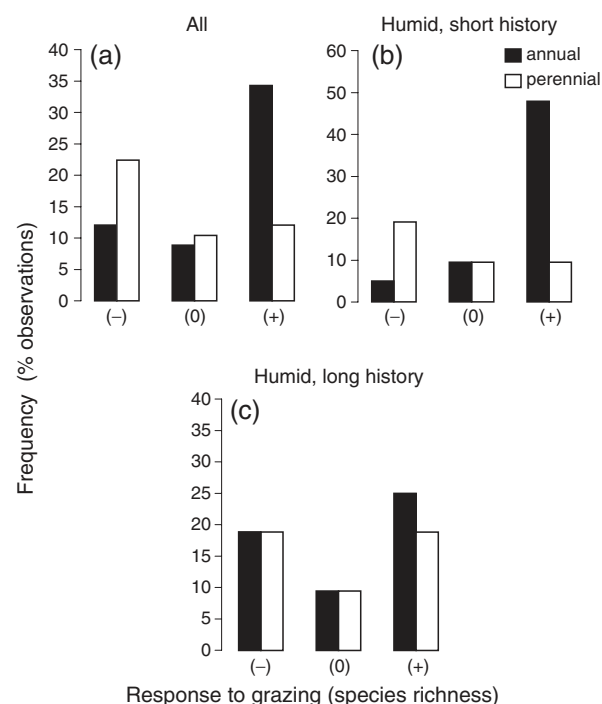


Fig. 2 Relative frequency of observations in which the richness of annual and perennial plants decreased (-), did not change (0) or increased (+) with grazing. (a) Considering all sites, and controlling for the effects of precipitation (dry or humid) and evolutionary history of grazing (short or long); $P = 0.013$, $n = 65$; Cochran-Mantel-Haenszel Association test. (b) In humid systems with short evolutionary history of grazing; $P = 0.038$, $n = 21$; G^2 -test. (c) In humid systems with long evolutionary history of grazing; $P = 0.922$, $n = 32$; G^2 -test.

Habit

Globally, there was a significant association between the direction of response to grazing and habit. In all systems erect plants tended to respond negatively to grazing, and prostrate plants tended to respond positively (Fig. 4). Trends observed in dry and humid systems were similar in direction, but those in dry systems were weaker and only marginally significant. Trends in short- and long-history systems were similar in direction and magnitude. There were insufficient observations to reject the null hypothesis in dry sites with a short history of herbivory or to analyse dry sites with a long history of herbivory.

Architecture

There was a significant association between the direction of response to grazing and shoot architecture. Positive responses of rosettes and stoloniferous plants, and negative responses of tussock graminoids were reported most frequently (Fig. 5a). There was no consistent trend

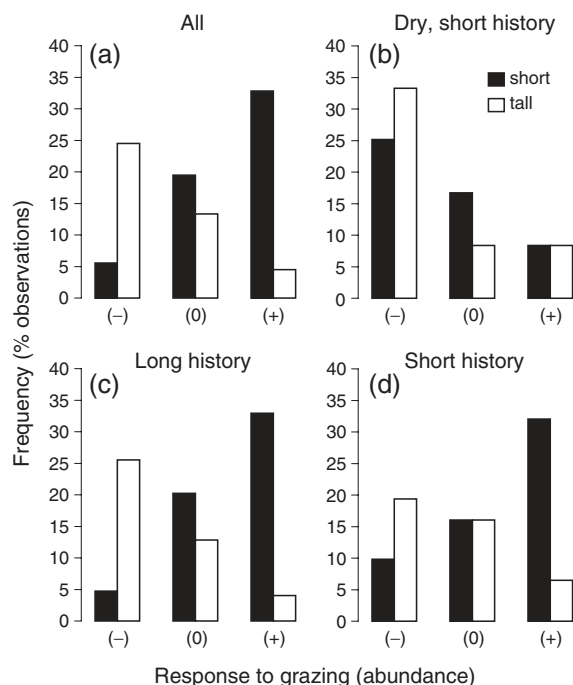


Fig. 3 Relative frequency of observations in which the abundance of plants with different height decreased (–), did not change (0), or increased (+) with grazing. (a) Considering all observations, and controlling for the effects of precipitation (dry or humid) and evolutionary history of grazing (short or long); $P < 0.0001$, $n = 180$; Cochran–Mantel–Haenszel Association test. (b) In dry systems with short evolutionary history of grazing; $P = 0.785$, $n = 12$; G^2 -test. (c) In systems with long evolutionary history of grazing; $P < 0.0001$, $n = 149$; G^2 -test. (d) In systems with short evolutionary history of grazing; $P = 0.049$, $n = 31$; G^2 -test.

in the response of plants with leafy stems. These global relationships were influenced mostly by sites from humid systems (crf. Fig. 5b and c) and systems with a long history of grazing (crf. Fig. 5d and e). There were insufficient data to run the analysis in the dry sites with a long history and humid sites with a short history.

When only graminoids were considered, the tendencies described above were maintained. Positive response of stoloniferous graminoids, and negative response of tussock graminoids to grazing were reported most frequently (Fig. 5f). Again, these results were driven mostly by humid systems and systems with a long history of grazing. There was no significant trend in dry systems and there were insufficient short-history cases for analysis. When only forbs were considered, no significant trend of response of rosettes vs. plants with leafy stem was detected.

Growth form

Globally, there was a significant association between the direction of response to grazing and growth form

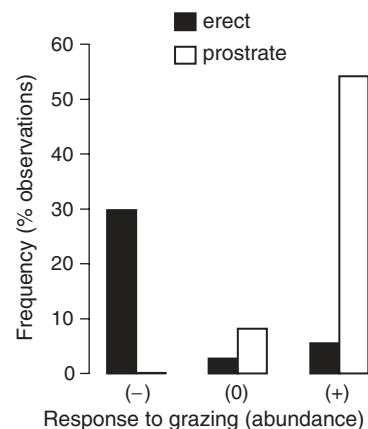


Fig. 4 Relative frequency of observations in which the abundance of plants with different habit decreased (–), did not change (0), or increased (+) with grazing, considering all observations, and controlling for the effects of precipitation and evolutionary history of grazing; $P < 0.0001$, $n = 37$; Cochran–Mantel–Haenszel Association test.

(Fig. 6). Forbs and woody species most frequently showed neutral responses to grazing, whereas graminoids had predominantly neutral or negative responses. There was insufficient information to draw conclusions on the response of herbaceous legumes. The association between response to grazing and growth form remained significant among different combinations of precipitation and grazing history, except for humid systems with short herbivory history that displayed no significant trend. The direction of the response of the woody growth form was the least consistent across climate and history combinations. However, the most common response of woody plants to grazing was a neutral response, both at the level of the entire dataset (Fig. 6) or under different combinations of precipitation and evolutionary herbivory history.

Palatability

We detected a significant association between the direction of response to grazing and palatability, with an increase in unpalatable plants being most frequently reported ($P = 0.005$, Appendix C). However, most observations came from systems with a long grazing history and so we cannot say whether this relationship holds under other conditions. In addition, when examining individual combinations of precipitation and grazing history, this result appeared to be accounted for by the bias of the data towards dry systems with a long herbivory history (mainly African). In regions with a long history and humid climate the relationship was not significant.

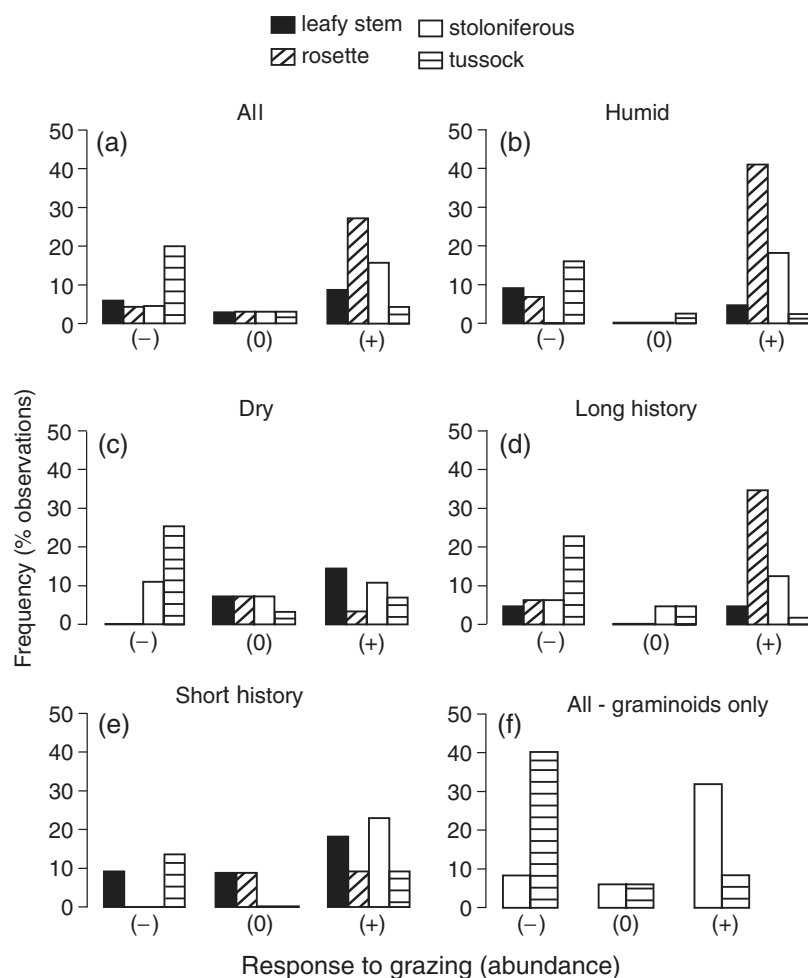


Fig. 5 Relative frequency of observations in which the abundance of plants with different architecture (leafy stem, rosette, stoloniferous, tussock) decreased (-), did not change (0), or increased (+) with grazing. (a) Considering all observations, and controlling for the effects of precipitation (dry or humid) and evolutionary history of grazing (short or long); $P = 0.002$, $n = 71$; Cochran–Mantel–Haenszel Association test. (b) In humid systems; $P < 0.001$, $n = 44$; G^2 -statistic. (c) In dry systems; $P = 0.032$, $n = 27$. (d) In systems with long evolutionary history of grazing; $P < 0.001$, $n = 49$. (e) In systems with short evolutionary history of grazing; $P = 0.040$, $n = 22$. (f) Considering only graminoids with different architecture (stoloniferous, tussock), taking into account all observations, and controlling for the effects of precipitation and evolutionary history of grazing; $P = 0.002$, $n = 35$; Cochran–Mantel–Haenszel Association test.

Origin

The association between origin and the direction of grazing response was not significant. The most common response to grazing was no change in the richness of both native and exotic species. In the case of abundance, however, there was a weak trend for a positive response of exotic plants and a negative response of native plants to grazing. The lack of clear trends may result from the low number of observations (23). These observations were strongly biased towards humid systems with short history of grazing (mostly Australasian systems), and even in this subset of observations the trend was not significant. No test could be run for

the other combinations of precipitation and grazing history.

Discussion

Data and publication biases

Our knowledge of the effect of grazing at a global scale is restricted to a surprisingly small number of plant traits. Even for these basic traits, there were insufficient data to adequately test all combinations of precipitation and history of herbivory. Data availability varied markedly across regions for several reasons. Regional studies

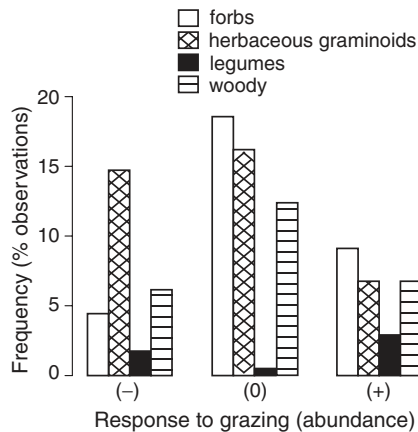


Fig. 6 Relative frequency of observations in which the abundance of plants with different growth forms (forbs, graminoids, legumes, and woody plants) decreased (–), did not change (0), or increased (+) with grazing, considering all observations and controlling for the effects of precipitation (dry or humid) and evolutionary history of grazing (short or long); $P < 0.0001$, $n = 341$; Cochran–Mantel–Haenszel Association test.

naturally focus on locally important traits and attributes and so do not record less important traits in a systematic way. Traits or attributes that are absent, or do not vary much, are ignored. For example, 74% of our data on exotics came from humid regions with a short evolutionary history of herbivory where exotic invasions are a conservation issue. Similarly, data on unpalatable plants are collected where they are a problem, for example in Africa and Australia. Such failures to report on specific traits represent a serious obstacle for literature-based syntheses in general (Díaz *et al.*, 2002). In addition, because of biogeographical reasons, some combinations of grazing history and climate are more frequent than others in the planet. This is an unavoidable constraint in most global-scale studies, and available statistical techniques can overcome it only to a certain degree. However, the consistency among independent studies is encouraging. For example, for dry areas with short herbivory history the findings of Milchunas & Lauenroth (1993) and those of this study are in agreement, despite the fact that the former is biased towards North American sites, and the latter towards Australian sites. We conclude that more investigations of plant trait responses to grazing are needed that follow a common framework and are conducted in a variety of locations (Díaz *et al.*, 2002). Using common lists of traits across research groups would ensure standardization of trait measurement in different systems of the world. This would alleviate the problem of unreported responses, or lack of response because species with the relevant attribute are simply absent. Publications describing consensus trait lists (e.g. Weiher

et al., 1999), and standard methods of measurement are available (Cornelissen *et al.*, 2003; Knevel *et al.*, 2005). Shortlists of traits that should be favoured or disfavoured by grazing under different environmental contexts, with implications for ecosystem functioning, have also been proposed (Coley *et al.*, 1985; Grime *et al.*, 1996), and validated in a small number of studies (Pérez-Harguindeguy *et al.*, 2003; Duru *et al.*, 2004). Chief among these traits are leaf nitrogen content, toughness and specific area. These traits are also implicated in primary productivity, nutrient cycling and trophic transfer (e.g. Lavorel & Garnier, 2002; Díaz *et al.*, 2004; Garnier *et al.*, 2004), and are applicable from the local to the transcontinental scale (Díaz *et al.*, 2004; Wright *et al.*, 2004). Substantial progress can also be made by reanalysing existing species-based studies. For example, the abundant phytosociological data on responses of plant communities to grazing available from Europe could be reanalysed incorporating information from the trait datasets available (e.g. Fitter & Peat, 1994; Hodgson *et al.*, 1995; Knevel *et al.*, 2003).

Global and context-specific patterns of trait response to grazing

Despite the inherent limitations of the data our results show that there are traits that exhibit consistent response to grazing, provided that the general context (e.g. climate and evolutionary history of herbivory) is taken into account. We can, therefore, use these results to assess whether predictions of the different conceptual models of plant trait response to grazing (Table 1) are supported at the global scale (Table 3).

Life history. In general, annuals are favoured by grazing and perennials are disadvantaged. This is consistent with the predictions of the range-succession, generalized, and CSR models. Although dry regions with a short evolutionary history of grazing conformed to this pattern, dry regions with a long history showed no consistent pattern in annuals and perennials. The prediction of the CSR and generalized models that the increased abundance of annuals should be more marked in humid systems is confirmed by our results.

Canopy height. Grazing favours short plants irrespective of climate and grazing history. This is consistent with the predictions of all the models. There is no evidence that short plants are more favoured by grazing in dry systems, as suggested by the CSR model. Rather, the response to grazing appeared more marked in humid systems and in systems with a long herbivory history, as predicted by the generalized model.

Table 3 Summary of plant trait responses to grazing under different combinations of precipitation and herbivory history

Trait	Is there any overall effect of grazing on the trait, controlling for precipitation and history?	Does precipitation by itself influence the direction of the response to grazing?	Does history of herbivory by itself influence the direction of the response to grazing?	Do different combinations of history and precipitation influence the direction of response to grazing?
Life history (abundance)	Yes	No	No	Yes (neutral response most frequent in dry + long history)
Life history (sp. richness)	Yes	Uncertain	Yes	Yes (ns difference in humid + long history)
Canopy height (abundance)	Yes	No	Uncertain	Yes (ns difference in dry + short history)
Habit (abundance)	Yes	No	No	Uncertain
Architecture (abundance)	Yes	Uncertain	Uncertain	na
Growth form (abundance)	Yes	No	Yes	Yes (ns difference in humid + short history)
Growth form (sp. richness)	No	na	na	na
Palatability (abundance)	Yes	Yes	Uncertain	na
Origin (abundance)	Uncertain	na	na	na
Origin (sp. richness)	No	na	na	na

'Uncertain' denotes that a trend existed, but it may have been nonsignificant due to small sample size, or that changes under different situations occurred in the same direction, but were much stronger in one case than in the other. na, not assessed due to lack of data. See text and Appendix C for details.

Habit. Grazing promotes increases in prostrate plant abundance and decreases in erect plants. This supports the predictions of the range-succession, generalized, CSR and physiological models. There is no indication that responses are stronger in dry systems, as predicted by the CSR model. Again, the response seems marginally stronger in humid systems and in systems with long herbivory history, as predicted by the generalized model. The low significance values obtained for dry and short-history systems may reflect small sample sizes.

Architecture. Grazing increases the abundance of stoloniferous and rosette plants. The increase in stoloniferous plants is a prediction of all the models that dealt with architecture (Table 1). The results also support the prediction of the generalized model that this effect is stronger in humid sites with long herbivory history.

Growth form. According to our results, grazing does not uniformly favour forbs, graminoids or woody species. Only two models provide explicit predictions of the impact of grazing on growth form. Neither the prediction of the range-succession model that forb and woody species abundance increases with grazing nor the prediction of the generalized model (Milchunas & Lauenroth, 1993) that graminoids increase with grazing is supported by this study. Instead, our results suggest that neutral responses of both groups are widespread. It is evident from the conflicting predictions that this is a complex issue, and while we have detected different responses in different systems, it appears that 'graminoids' as a functional group is too general. The analysis of architecture within graminoids shows negative responses of tussocks and positive responses of stoloniferous grasses, suggesting a wide range of grazing responses within this broad group.

The fact that grazing does not favour woody species, with neutrality being the most common response in our study, seems surprising considering the extensive literature on woody encroachment (e.g. Milchunas & Lauenroth, 1993; Scholes & Archer, 1997; Skarpe, 2000; but see Veski *et al.*, 2004). Grazing did not increase shrub abundance even in dry rangelands for which the prediction is most commonly made (e.g. Milton *et al.*, 1994), perhaps because cases of grazing-induced shrub encroachment are balanced by cases where grazing-sensitive shrubs are reduced by grazing. Other explanations may be irreversible shrub increases (Westoby *et al.*, 1989), or the alternation of positive and negative interactions between herbaceous and woody plants at different life cycle stages in a mosaic landscape (Olff *et al.*, 1999). Finally, changes in grazing

and woody vegetation are intimately linked with changes in fire regimes, so that it may not be possible to distinguish the separate rather than synergistic effects of climate, fire and grazing (Bond *et al.*, 2003).

Palatability. Grazing leads to increases in unpalatable plants, and the effect is stronger in dry systems than in humid systems. This is consistent with the predictions of all four conceptual models that included palatability. This trend however seems to be driven mostly by dry systems with long herbivory history. Fewer studies in dry regions with short herbivory history (e.g. Landsberg *et al.*, 2002; Vesik *et al.*, 2004) have analysed palatability. The evidence from studies in humid regions with long herbivory history was inconclusive. This seems to disagree with the theory and observations that in productive areas with a long herbivory history, grazing increases the abundance of palatable plants (e.g. McNaughton, 1984). However, this discrepancy may partly result from the pooling together of palatability traits and so our results do not provide clear-cut evidence of the effect of grazing history on palatability.

Origin. There were too few studies available to obtain solid conclusions on the impact of grazing on exotic plant invasion. However, as predicted by the generalized model exotics tended to increase under grazing in regions with a short history of herbivory, particularly in humid climates. The model predicts relatively less invasion by exotics under grazing where there has been a long herbivory history, but there were insufficient data to test this.

Our results supported all five conceptual models of plant trait response to grazing at the global scale. However, the generalized model was the one which best explained the patterns observed under different combinations of climate and herbivory history. There was no case where the direction of the response was changed, but response strength varied depending on climate and herbivory history. In total, our results suggest that response to grazing is modulated by these two interacting factors. Although the influence of productivity on plant grazing response has been widely recognized (e.g. Proulx & Mazumder, 1998; Milchunas & Noy-Meir, 2002), that of herbivory history has been largely ignored and very few empirical studies have taken it into consideration (e.g. Naveh & Whittaker, 1979; Milchunas & Lauenroth, 1993; Díaz *et al.*, 2001; Milchunas & Noy-Meir, 2002; Adler *et al.*, 2004; Cingolani *et al.*, 2005). Our results indicate that a conceptual framework for the investigation of plant trait response to grazing, both

under specific regional situations and as part of transregional comparisons, should incorporate both climatic and historical contexts.

Implications for plant functional classifications for large-scale vegetation models

Our study, the first meta-analysis to assess plant trait responses to grazing at a worldwide scale, suggests that (1) plant trait responses to grazing could improve the ability of current large-scale vegetation models; and (2) care should be taken when attempting to project vegetation response to climate in grazed ecosystems, as these two factors interact in driving the functional composition of vegetation.

What would be the minimum set of traits that would allow us to incorporate plant responses to grazing in predictions of climate change impacts? On the basis of Table 3, we confirm that the distinction between woody and herbaceous plants made by current large-scale models is useful and that a minimum set of easily accessible traits for herbaceous plants should include life history and height or habit. The distinction between woody and herbaceous plants is included in DGVMs, but the models generally do not subdivide herbaceous plants on the basis of life histories or height (see e.g. Prentice *et al.*, 2007). Leaf traits of shrubs, such as leaf size, specific area and toughness are important to capture climatic response (Barboni *et al.*, 2004), and possibly for grazing response and effects on biogeochemistry. However no leaf trait could be analysed in this study due to the paucity of data. Among herbaceous plants, grasses are often classified in global models as C3 vs. C4 (e.g. Cramer *et al.*, 2001). Subgroups should distinguish within these two main climatically and biogeochemically relevant groups to account for grazing response. A minimal classification would divide the C3 and C4 groups into annual vs. perennial, and then within each of these subgroups, distinguish between tussock vs. stoloniferous grasses.

Our study also indicates that to incorporate grazing impacts in climate change predictions it seems necessary to develop rules for specific climate regimes (e.g. dry vs. humid climates). Given that differences in response between dry and humid climates are thought to reflect ANPP (Milchunas *et al.*, 1988; Milchunas & Lauenroth, 1993), it would also be possible to formulate rules as functions of model-simulated ANPP in the absence of grazing (potential vegetation). Our analyses indicate that it will also be necessary to map grazing histories globally in order to predict the correct response to grazing. This seems feasible provided broad categories are applied. However, more detailed information on grazing regime (e.g. frequency, intensity)

Table 4 Plant functional types proposed for inclusion in DGVMs that take grazing into consideration

Humid – long grazing history*	Humid – short grazing history*†	Dry – long grazing history*	Dry – short grazing history*†
Woody evergreen	Woody evergreen	Woody evergreen	Woody evergreen
Woody deciduous	Woody deciduous	Woody deciduous	Woody deciduous
Graminoid short C ₃ annual prostrate	Graminoid short C ₃ annual prostrate	Graminoid short C ₃	Graminoid C ₃ annual prostrate
Graminoid short C ₃ annual erect	Graminoid short C ₃ annual erect	Graminoid short C ₄	Graminoid C ₃ annual erect
Graminoid short C ₃ perennial prostrate	Graminoid short C ₃ perennial prostrate	Graminoid tall C ₃	Graminoid C ₃ perennial prostrate
Graminoid short C ₃ perennial erect	Graminoid short C ₃ perennial erect	Graminoid tall C ₄	Graminoid C ₃ perennial erect
Graminoid short C ₄ annual prostrate	Graminoid short C ₄ annual prostrate	Forb short prostrate	Graminoid C ₄ annual prostrate
Graminoid short C ₄ annual erect	Graminoid short C ₄ annual erect	Forb short erect	Graminoid C ₄ annual erect
Graminoid short C ₄ perennial prostrate	Graminoid short C ₄ perennial prostrate	Forb tall	Graminoid C ₄ perennial prostrate
Graminoid short C ₄ perennial erect	Graminoid short C ₄ perennial erect		Graminoid C ₄ perennial erect
Graminoid tall C ₃ annual	Graminoid tall C ₃ annual		Forb annual prostrate
Graminoid tall C ₃ perennial	Graminoid tall C ₃ perennial		Forb annual erect
Graminoid tall C ₄ annual	Graminoid tall C ₄ annual		Forb perennial prostrate
Graminoid tall C ₄ perennial	Graminoid tall C ₄ perennial		Forb perennial erect
Forb short annual prostrate	Forb short annual prostrate		
Forb short annual erect	Forb short annual erect		
Forb short perennial prostrate	Forb short perennial prostrate		
Forb short perennial erect	Forb short perennial erect		
Forb tall annual	Forb tall annual		
Forb tall perennial	Forb tall perennial		

Relevant functional types are listed for each climate × grazing history category. See text for further explanation.

*There was not sufficient data in our database to assess whether the distinction between erect and prostrate forbs was relevant in any of the combinations of climate and grazing history.

†There was no significant difference in the grazing responses of erect and prostrate graminoids, but the number of cases was low. Therefore, and taking a conservative approach, their inclusion is suggested until more information is available.

DGVM, Dynamic global vegetation model.

may be needed for finer-scale regional assessments (Cingolani *et al.*, 2005).

In practice, we propose a three-step approach to refining plant functional type (PFT) classifications of DGVMs in order to account for grazing response and effects. First, ANPP needs to be simulated using classical life form and phenology/metabolism based classifications, yielding a global or regional map of ANPP. This could then be reclassified into two productivity categories using an agreed threshold (e.g. Milchunas *et al.*, 1988; Milchunas & Lauenroth, 1993). Second, a four category map of productivity \times grazing history would be obtained by combining this productivity map with a map of grazing history (short and long). As a third and final step, a different set of relevant PFTs could be applied to each climate \times grazing history combination, on the basis of our results (Table 4). The relevant PFTs listed in Table 4 were obtained by subdividing, for each category of regional climate \times grazing history, the PFTs based on combinations of life form and phenology that are commonly used by DGVMs. The traits used for subdivision within each PFT were those shown as significant by our analyses for each climate \times grazing history category. The additional traits for herbaceous plants were: life form, life history, plant height, and architecture. Under dry climates the number of relevant traits, and therefore of PFTs, was reduced, especially with a long grazing history. Region-specific PFTs have already been implemented in some DGVMs (e.g. Barboni *et al.*, 2004), suggesting that the incorporation of these refinements in future developments should not pose serious technical challenges.

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References

- Adler PB, Milchunas DG, Lauenroth WK *et al.* (2004) Functional traits of graminoids in semi-arid steppes: a test of grazing histories. *Journal of Applied Ecology*, **41**, 653–663.
- Agresti A (2002) *Categorical Data Analysis*, 2nd edn. John Wiley and Sons, New York.
- Agustí J, Antón M (2002) *Mammoths, Sabertooths, and Hominids – 65 Million Years of Mammalian Evolution in Europe*. Columbia University Press, New York.
- Arnold JF (1955) Plant life-form classification and its use in evaluating range conditions and trend. *Journal of Range Management*, **8**, 176–181.
- Atkinson IAE, Greenwood RM (1989) Relationships between moas and plants. *New Zealand Journal of Ecology*, **12**, 67–96.
- Bachelet D, Lenihan JM, Daly C *et al.* (2000) Interactions between fire, grazing and climate change at Wind Cave National Park, SD. *Ecological Modelling*, **134**, 229–244.
- Barboni D, Harrison SP, Bartlein PJ *et al.* (2004) Relationships between plant traits and climate in the Mediterranean region: a pollen data analysis. *Journal of Vegetation Science*, **15**, 635–646.
- Bock JH, Jolls CL, Lewis AC (1995) The effects of grazing on alpine vegetation: a comparison of the central Caucasus, Republic of Georgia, with the Colorado Rocky Mountains, USA. *Arctic and Alpine Research*, **27**, 130–136.
- Bond WJ (2005) Large parts of the world are brown or black: a different view on the 'Green World' hypothesis. *Journal of Vegetation Science*, **16**, 261–266.
- Bond WJ, Midgley GF, Woodward FI (2003) The importance of low atmospheric CO₂ and fire in promoting the spread of grasslands and savannas. *Global Change Biology*, **9**, 973–982.
- Borrero LS (1996) The Pleistocene–Holocene transition in southern South America. In: *Humans at the End of the Ice Age* (eds Strauss LG, Eriksen BV, Erlandson JM, Yesner DR), pp. 339–354. Plenum Press, New York.
- Briske D (1996) Strategies of plant survival in grazed systems: a functional interpretation. In: *The Ecology and Management of Grazed Systems* (eds Hodgson J, Illius A), pp. 37–67. CAB International, Wallingford.
- Briske D, Richards J (1995) Plant responses to defoliation: a physiological, morphological and demographic evaluation. In: *Wildland Plants: Physiological Ecology and Developmental Biology* (eds Bedunah D, Sosebee R), pp. 635–710. Society for Range Management, Denver.
- Cingolani A, Noy-Meir I, Díaz S (2005) Grazing effects on rangeland diversity: diversity–intensity and state and transition models. *Ecological Applications*, **15**, 757–773.
- Coley PD, Bryant JP, Chapin FS (1985) Resource availability and plant anti-herbivore defense. *Science*, **230**, 895–899.
- Cornelissen JHC, Lavorel S, Ganier E (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–380.
- Cramer W, Bondeau A, Woodward FI *et al.* (2001) Global response of terrestrial ecosystem structure and function to CO₂ and climate change: results from six dynamic global vegetation models. *Global Change Biology*, **7**, 357–373.
- Daly C, Bachelet D, Lenihan JM *et al.* (2000) Dynamic simulation of tree-grass interactions for global change studies. *Ecological Applications*, **10**, 449–469.
- Day TA, Detling JK (1990) Grassland patch dynamics and herbivore grazing preference following urine deposition. *Ecology*, **71**, 180–188.

- Díaz S, Hodgson JG, Thompson K *et al.* (2004) The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science*, **15**, 295–304.
- Díaz S, McIntyre S, Lavorel S, Pausas JG (2002) Does hairiness matter in Harare? Resolving controversy in global comparisons of plant trait responses to ecosystem disturbance. *New Phytologist*, **154**, 7–9.
- Díaz S, Noy-Meir I, Cabido M (2001) Can grazing response of herbaceous plants be predicted from simple vegetative traits? *Journal of Applied Ecology*, **38**, 497–508.
- Duru M, Cruz P, Magda D (2004) Using plant traits to compare sward structure and composition of grass species across environmental gradients. *Applied Vegetation Science*, **7**, 11–18.
- Dyksterhuis EJ (1949) Condition and management of rangelands based on quantitative ecology. *Journal of Range Management*, **2**, 104–115.
- Eastman JL, Coughenour MB, Pielke RA (2001) Does grazing affect regional climate? *Journal of Hydrometeorology*, **2**, 243–253.
- Edelstein G, Milevsky I (1994) The rural settlement of Jerusalem re-evaluated. *Palestine Exploratory Quarterly*, **126**, 1–23.
- Fitter AH, Peat HJ (1994) The ecological flora database. *Journal of Ecology*, **82**, 415–425.
- Franklin WL (1982) Biology, ecology and relationship to man of the South American camelids. In: *Mammalian Biology in South America* (eds Mares MA, Genoways HH), pp. 457–489. Pymatuning Laboratory of Ecology, University of Pittsburgh, Pittsburgh.
- Garnier E, Cortez J, Billès G *et al.* (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, **85**, 2630–2637.
- Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, **111**, 1169.
- Grime JP (1990) Mechanisms promoting floristic diversity in calcareous grasslands. In: *Calcareous Grasslands – Ecology and Management* (eds Hillier SH, Walton DWH, Wells DA), pp. 51–56. Bluntisham Books, Huntingdon.
- Grime JP (2001) *Plant Strategies, Vegetation Processes, and Ecosystem Properties*, 2nd edn. John Wiley and Sons, Chichester.
- Grime JP, Cornelissen JHC, Thompson K *et al.* (1996) Evidence of a causal connection between anti-herbivore defence and the decomposition rate of leaves. *Oikos*, **77**, 489–494.
- Gurevitch J, Hedges LV (1999) Statistical issues in ecological meta-analysis. *Ecology*, **80**, 1142–1149.
- Hermes DA, Mattson WJ (1992) The dilemma of plants: to grow or defend. *The Quarterly Review of Biology*, **67**, 283–335.
- Hodgson JG, Grime JP, Hunt R *et al.* (1995) *The Electronic Comparative Plant Ecology*. Chapman and Hall, London.
- Huntly N (1991) Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics*, **22**, 477–503.
- Knevel I, Bekker R, Bakker J *et al.* (2003) Life-history traits of the Northwest European flora: the LEDA database. *Journal of Vegetation Science*, **14**, 611–614.
- Knevel I, Bekker RM, Kunzmann D, *et al.* (2005) *The LEDA Traitbase Collecting and Measuring Standards*. Scholma Bruk B.V., Bedum.
- Köppen W (1918) Klassifikation der Klimate nach Temperatur, Niederschlag, und jahres lauf. *Petermann's Mitteilungen*, **64**, 193–203, 243–248.
- Landsberg J, James C, Maconochie J *et al.* (2002) Scale-related effects of grazing on native plant communities in an arid rangeland region of South Australia. *Journal of Applied Ecology*, **39**, 427–444.
- Landsberg J, O'Connor T, Freudenberger D (1999) The impacts of livestock grazing on biodiversity in natural ecosystems. In: *Nutritional Ecology of Herbivores* (eds Jung HJG, Fahey GC Jr), pp. 752–777. American Society of Animal Science, IL, USA.
- Lauenroth WK (1979) Grassland primary production: North American grasslands in perspective. In: *Perspectives in Grassland Ecology* (ed. French NR), pp. 3–24. Springer-Verlag, New York.
- Lavorel S, Díaz S, Cornelissen H *et al.* (2007) Plant functional types: are we getting any closer to the Holy Grail? In: *Terrestrial Ecosystems in a Changing World* (eds Canadell J, Pataki D, Pitelka L), pp. 171–186. Springer-Verlag, New York.
- Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits – revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.
- Lavorel S, McIntyre S, Landsberg J *et al.* (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology and Evolution*, **12**, 474–478.
- McGuire AD, Sitch S, Clein JS *et al.* (2001) Carbon balance of the terrestrial biosphere in the twentieth century: analyses of CO₂, climate and land use effects with four process-based ecosystem models. *Global Biogeochemical Cycles*, **15**, 183–206.
- McNaughton SJ (1984) Grazing lawns: animals in herds, plant form, and coevolution. *The American Naturalist*, **124**, 863–886.
- Milchunas DG, Lauenroth WK (1993) A quantitative assessment of the effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, **63**, 327–366.
- Milchunas DG, Noy-Meir I (2002) Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos*, **99**, 113–130.
- Milchunas DG, Sala OE, Lauenroth WK (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. *The American Naturalist*, **132**, 87–106.
- Milton SJ, Dean RJ, du Plessis MA *et al.* (1994) A conceptual model of arid rangeland degradation. *BioScience*, **44**, 70–76.
- Mooney HA, Hobbs RJ (2000) *Invasive Species in a Changing World*. Island Press, Washington, DC.
- Naveh Z, Whittaker R (1979) Structural and floristic diversity of shrublands and woodlands in Northern Israel and other Mediterranean regions. *Vegetatio*, **43**, 5–21.
- Olf H, Vera FWM, Bokdam J *et al.* (1999) Shifting mosaics in grazed woodlands driven by the alternation of plant facilitation and competition. *Plant Biology*, **1**, 127–137.
- Pérez-Harguindeguy N, Díaz S, Cabido M (2003) Leaf traits and herbivore selection in the field and in cafeteria experiments. *Austral Ecology*, **28**, 642–650.
- Prentice IC, Bondeau A, Cramer W *et al.* (2007) Dynamic global vegetation models: tools to understand the biosphere. In: *Terrestrial Ecosystems in a Changing World* (eds Canadell J, Pataki D, Pitelka L), pp. 177–192. Springer-Verlag, New York.

- Proulx M, Mazumder A (1998) Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology*, **79**, 2581–2592.
- Scholes R, Archer S (1997) Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, **28**, 517–544.
- Sitch S, Smith B, Prentice IC *et al.* (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, **9**, 161–185.
- Skarpe C (2000) Desertification, no-change or alternative states: can we trust simple models on livestock impact in dry rangelands? *Applied Vegetation Science*, **3**, 201–268.
- Stohlgren TJ, Binkley D, Chong GW (1999) Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs*, **69**, 25–46.
- van der Hammen T (1983) The palaeoecology and palaeogeography of savannas. In: *Tropical Savannas* (ed. Bourlière F), pp. 19–36. Elsevier, Amsterdam.
- Vesk PA, Leishman M, Westoby M (2004) Simple traits do not predict grazing response in Australian dry shrublands and woodlands. *Journal of Applied Ecology*, **41**, 22–31.
- Vesk PA, Westoby M (2001) Predicting plant species' response to grazing. *Journal of Applied Ecology*, **38**, 897–909.
- Wardle DA, Bardgett RD (2004) Human-induced changes in large herbivorous mammal density: the consequences for decomposers. *Frontiers in Ecology and the Environment*, **2**, 145–153.
- Weiher E, van der Werf A, Thompson K *et al.* (1999) Challenging theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science*, **10**, 609–620.
- Westoby M (1989) Selective forces exerted by vertebrate herbivores on plants. *Trends in Ecology and Evolution*, **4**, 115–117.
- Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, **199**, 213–227.
- Westoby M (1999) The LHS strategy in relation to grazing and fire. In: *Proceedings VI International Rangeland Congress* (eds Eldridge D, Freudenberger D), pp. 893–896. International Rangeland Congress Inc., Townsville.
- Westoby M, Walker B, Noy-Meir I (1989) Opportunistic range management for rangelands not at equilibrium. *Journal of Range Management*, **42**, 265–273.
- Wright IJ, Reich PB, Westoby M *et al.* (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.
- Zimov S, Chuprynin V, Oreshlo A *et al.* (1995) Steppe-tundra transition – a herbivore-driven biome shift at the end of the Pleistocene. *The American Naturalist*, **146**, 765–794.
- Research Institute, Department of Agricultural Technical Services. **40**, 1–128.
- Barnes DL (1989) Reaction of three veld grasses to different schedules of grazing and resting. I. Patterns of shoot growth. *South African Journal of Plant and Soil*, **6**, 1–7.
- Belsky AJ (1992) Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *Journal of Vegetation Science*, **3**, 187–200.
- Bosch OJH (1988) Degradation of the semi-arid grasslands of Southern Africa. *Journal of Arid Environments*, **16**, 165–175.
- Boultonwood JN, Rodel MGW (1981) Effects of stocking rate and burning frequency on *Brachystegia*/*Julbernardia* veld in Zimbabwe. *Proceedings of the Grassland Society of Southern Africa*, **16**, 111–115.
- Breman H, Cissé AM, Djiteye MA, *et al.* (1979) Pasture dynamics and forage availability in the Sahel. *Israel Journal of Botany*, **28**, 227–251.
- Breman H, de Ridder N (1991) *Manuel Sur les Pâturages des Pays Sahéliens*. ACCT-CTA-Karthala, Paris and Wageningen, 485 pp.
- Campbell A, Child G (1971) The impact of man on the environment of Botswana. *Botswana Notes and Records*, **3**, 91–110.
- Cissé AM (1986) *Dynamique de la Strate Herbacée des Pâturages de la Zone Sud-sahélienne*. Agricultural University of Wageningen, the Netherlands.
- Fuls ER (1992) Ecosystem modification created by patch-overgrazing in semi-arid grassland. *Journal of Arid Environment*, **23**, 59–69.
- Fuls ER, Bosch JH (1991) The influence of below-average rainfall on the vegetational traits of patch-grazed semi-arid grassland. *Journal of Arid Environments*, **21**, 13–20.
- Georgiadis NJ, McNaughton SJ (1988) Interactions between grazers and a cyanogenic grass, *Cynodon plecostachyus*. *Oikos*, **51**, 343–350.
- Heady HF (1966) Influence of grazing on the composition of *Themeda triandra* grassland, East Africa. *Journal of Ecology*, **54**, 705–727.
- Le Houerou HN (1986) *The Grazing Land Ecosystems of the African Sahel*. Springer Verlag, Berlin.
- McNaughton SJ, Tarrants JL, McNaughton MM, *et al.* (1985) Silica as a defense against herbivory and a growth promotor in African grasses. *Ecology*, **66**, 528–535.
- O'Connor TGO (1994) Composition and population responses of an African savanna grassland to rainfall and grazing. *Journal of Applied Ecology*, **31**, 155–171.
- Oba G (1992) Effects of controlled grazing on a degraded dwarf shrub, annual grass semidesert vegeta-

Appendix A

List of publications used as primary sources of data.

Africa

- Acocks JPH (1964) Karoo vegetation in relation to the development of deserts. In: *Ecological Studies of Southern Africa* (ed. Davies DHS), pp. 100–112. Junk, The Hague.
- Acocks JPH (1975) Veld Types of South Africa. Memoirs of the Botanical Survey of South Africa. Botanical

- tion type of northwestern Kenya. *Land Degradation and Rehabilitation*, **3**, 199–213.
- Oba G (1998) Effects of excluding goat herbivory on *Acacia tortilis* woodland around pastoralist settlements in northwest Kenya. *Acta Oecologica*, **19**, 395–404.
- Skarpe C (1986a) Plant community structure in relation to grazing and environmental changes along a north–south transect in western Kalahari. *Vegetatio*, **68**, 3–18.
- Skarpe C (1986b) *Vegetation Ecology of the Western Kalahari in Relation to Large Herbivore Grazing*. Acta Universitatis Upsaliensis No. 33, Uppsala.
- Skarpe C (1990) Shrub layer dynamics under different herbivore densities in an arid savanna, Botswana. *Journal of Applied Ecology*, **27**, 873–885.
- Strang RM (1974) Some man-made changes in successional trends in the Rhodesian highveld. *Journal of Applied Ecology*, **11**, 249–263.
- Strugnell RG, Pigott CD (1978) Biomass, shoot-production and grazing of two grasslands in the Rwenzori National Park, Uganda. *Journal of Ecology*, **66**, 73–96.
- van Vegten JA (1981) *Man-made Vegetation Changes: an example from Botswana's Savanna*. Working Paper No 40, National Institute of Development and Cultural Research. University of Botswana.
- van Vegten JA (1983) Thornbush invasion in a savanna ecosystem in eastern Botswana. *Vegetatio*, **56**, 3–7.
- Walter H (1954) Die verbuschung, eine erscheinung der subtropischen savannengebiete, und ihre ökologischen ursachen. *Vegetatio*, **5/6**, 6–10.
- Wells TCE, Sheail DF, Ball DF, *et al.* (1987) Ecological studies on the porton ranges: relationships between vegetation, soils and land-use history. *Journal of Ecology*, **64**, 589–626.
- Australasia*
- Allan B, O'Connor K, White J (1992) Grazing management of oversown tussock country 2. Effects on botanical composition. *New Zealand Journal of Agricultural Research*, **35**, 7–19.
- Fensham RJ (1998) The grassy vegetation of the darling downs, south-eastern Queensland, Australia. Floristics and grazing effects. *Biological Conservation*, **84**, 301–310.
- Fensham RJ, Skull SD (1999) Before cattle a comparative floristic study of *Eucalyptus* savanna grazed by macropods and cattle in North Queensland. *Biotropica*, **31**, 37–47.
- Foreman PW (1996) *Ecology of Native Grasslands on Victoria's Northern Riverine Plain*. La Trobe University, Melbourne.
- Lord J (1990) The maintenance of *Poa cita* grassland by grazing. *New Zealand Journal of Ecology*, **13**, 43–49.
- Lunt ID, Morgan JW (1999) Vegetation changes after 10 years of grazing exclusion and intermittent burning in a *Themeda triandra* (Poaceae) grassland reserve in south-eastern Australia. *Australian Journal of Botany*, **47**, 537–552.
- McIntosh P, Allen R (1998) Effects of enclosure on soils, biomass, plant nutrients, and vegetation, on unfertilised steeplands, upper Waitaki district, South Island, New Zealand. *New Zealand Journal of Ecology*, **22**, 209–217.
- McIntyre S, Lavorel S (1994) How environmental and disturbance factors influence species composition in temperate Australian grasslands. *Journal of Vegetation Science*, **5**, 373–384.
- McIntyre S, Lavorel S (2001) Livestock grazing in subtropical pastures: steps in the analysis of attribute response and plant functional types. *Journal of Ecology*, **89**, 209–226.
- McIntyre S, Lavorel S, Trémont RM (1995) Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. *Journal of Ecology*, **83**, 31–44.
- Navie SC, Rogers RW (1997) The relationship between attributes of plants represented in the germinable seed bank and stocking pressure in a semi-arid subtropical rangeland. *Australian Journal of Botany*, **45**, 1055–1071.
- Pettit NE, Froend RH, Ladd PG (1995) Grazing in remnant woodland vegetation: changes in species composition and life form groups. *Journal of Vegetation Science*, **6**, 121–130.
- Pettit NE, Ladd PG, Froend RH (1998) Passive clearing of native vegetation: livestock damage to remnant jarrah (*Eucalyptus marginata*) woodlands in western Australia. *Journal of the Royal Society of Western Australia*, **81**, 95–106.
- Rogers RW (1993) Selection for grasses with different carbon assimilation pathways under different sheep stocking pressures. *Australian Journal of Botany*, **41**, 327–331.
- Rogers RW (1995) Vegetative attributes, taxonomy, and character syndromes in grasses around a sheep camp on the northern tablelands of New South Wales. *Australian Journal of Botany*, **43**, 317–325.
- Rogers RW, Stride C (1997) Distribution of grass species and attributes of grasses near a bore drain in a grazed semi-arid subtropical grassland. *Australian Journal of Botany*, **45**, 919–927.
- Rose A, Platt K (1987) Recovery of northern fiordland alpine grassland after reduction in the deer population. *New Zealand Journal of Ecology*, **10**, 23–33.
- Trémont RM (1994) Life history attributes of plants in grazed and ungrazed grasslands on the northern

tablelands of New South Wales. *Australian Journal of Botany*, **42**, 511–530.

Central Asia

Fernandez-Gimenez M, Allen-Diaz B (1999) Testing a non-equilibrium model of rangeland vegetation dynamics in Mongolia. *Journal of Applied Ecology*, **36**, 871–885.

Wang S, Li Y (1999) Degradation mechanism of typical grassland in inner Mongolia. *Chinese Journal of Applied Ecology*, **10**, 437–441.

Zhang W (1995) *Vegetation dynamics in relation to livestock grazing in a semi-arid steppe in inner Mongolia*, Acta Universitatis Upsaliensis No. 130, Uppsala.

Mediterranean

Baudiere A, Simonneau J, Simonneau P (1973) *Contribution a l'Etude de la Végétation Halophile de la Plaine du Roussillon*. Communication 13, pp. 162. Laboratoire de Botanique Méditerranéenne et Pyrénéo-Alpine, Groupe de Recherches interdisciplinaire sur les terrains salés, Perpignan, France.

Debussche M, Escarré J, Lepart J, *et al.* (1996) Changes in Mediterranean plant succession: old-fields revisited. *Journal of Vegetation Science*, **7**, 519–526.

Díaz S, Noy-Meir I, Cabido M (2001) Can grazing response of herbaceous plants be predicted from simple vegetative traits? *Journal of Applied Ecology*, **38**, 487–508.

Fernández-Alés R, Laffarga JM, Ortega F (1993) Strategies in Mediterranean grassland annuals in relation to stress and disturbance. *Journal of Vegetation Science*, **4**, 313–322.

Hadar L, Noy-Meir I, Perevolotsky A (1999) The effect of shrub clearing on the composition of a Mediterranean plant community: functional groups vs. species. *Journal of Vegetation Science*, **10**, 673–682.

Joffre R (1987) *Contraintes du Milieu et Réponses de la Végétation Herbacée dans les Dhesas de la Sierra Norte (Andalousie, Espagne)*. Université des Sciences et Techniques du Languedoc, Montpellier II.

Koutsidou E, Giourga C, Loumou A, Margaritis N (1994) *Vegetation recovery in grazing exclosures in Greece*. Medallus Working Paper 18, <http://www.medalus.demon.co.uk/working.htm.1>

Lavorel S, McIntyre S, Grigulis K (1999) Plant response to disturbance in a Mediterranean grassland: how many functional groups? *Journal of Vegetation Science*, **10**, 661–672.

Montalvo J, Casado MA, Levassor C, *et al.* (1993) Species diversity patterns in Mediterranean grasslands. *Journal of Vegetation Science*, **4**, 213–222.

Noy-Meir I (1990) Responses of two semiarid rangeland communities to protection from grazing. *Israel Journal of Botany*, **39**, 431–442.

Noy-Meir I, Gutman M, Kaplan Y (1989) Responses of Mediterranean grassland plants to grazing and protection. *Journal of Ecology*, **77**, 290–310.

Ortega M, Levassor C, Peco B (1997) Seasonal dynamics of Mediterranean pasture seed banks along environmental gradients. *Journal of Biogeography*, **24**, 177–195.

Osem Y, Sternberg M, Perevolotsky A, *et al.* (1999) Species composition and abundance of annual plants in the seed bank and in the vegetation in a semiarid region in the northern Negev as affected by sheep grazing. *Ecology and Environment*, **5**, 180–189.

Pagnotta MA, Snaydon RW, Cocks PS (1997) The effects of environmental factors on components and attributes of Mediterranean grassland. *Journal of Applied Ecology*, **34**, 29–42.

Paraskevopoulos SP, Iatiou GD, Pantis JD (1994) Plant growth strategies in evergreen sclerophyllous shrublands (maquis) of central Greece. *Vegetatio*, **115**, 109–114.

Saidi MS (1998) *Evolution d'une Pelouse Post-ovine sous l'Effet du Pâturage du Cheval de Przewalski (Causse Méjean - Lozère)*. Université Paul Valéry, Montpellier.

Sternberg M, Gutman M, Perevolotsky A, *et al.* (2000) Vegetation response to grazing management in a Mediterranean herbaceous community: a functional group approach. *Journal of Applied Ecology*, **37**, 224–237.

Thiault B (1968) *Reconnaissance phyto-écologique des hautes terres des grands Causse lozériens*. Doc. no 37, pp. 117. Fasc. Annexes, CNRS, CEPE, Montpellier.

Tukel T (1984) Comparison of grazed and protected mountain steppe rangeland in Ulukisla, Turkey. *Journal of Range Management*, **37**, 133–139.

North America

Ashby MM, Hart RH, Forwood JR (1993) *Plant Community and Cattle Responses to Fifty Years of Grazing on Shortgrass Prairie*. Cheyenne, Wyoming.

Berg WA, Bradford JA, Sims PL (1997) Long-term soil nitrogen and vegetation change on sandhill rangeland. *Journal of Range Management*, **50**, 482–486.

Bethlenfalvay GJ, Dakessian S (1984) Grazing effects on mycorrhizal colonization and floristic composition or the vegetation on a semiarid range in northern Nevada. *Journal of Range Management*, **37**, 313–316.

Bonham CD, Trlica MJ (2003) *Forage: A Volumetric Measure of Desertification Trend in the Four Corners Region*. Final Report, USDA Competitive Grants Program for Antidesertification. Range Science Department, Colorado State University, Ft. Collins.

Brady WW, Stromberg MR, Aldon EF, *et al.* (1989) Response of a semidesert grassland to 16 years of rest from grazing. *Journal of Range Management*, **42**, 284–288.

Brand MD, Goetz H (1986) Vegetation of exclosures in southwestern North Dakota. *Journal of Range Management*, **39**, 434–437.

- Brotherson JD, Rushforth SR, Johansen JR (1983) Effects of long term grazing on cryptogam crust cover in Navajo National Monument, Arizona. *Journal of Range Management*, **38**, 579–581.
- Brown JR, Stuth JW (1993) How herbivory affects grazing tolerant and sensitive grasses in a central Texas grassland: integrating plant response across hierarchical levels. *Oikos*, **67**, 291–298.
- Canfield RH (1948) Perennial grass composition as an indicator of condition of southwestern mixed grass ranges. *Ecology*, **29**, 190–204.
- Chew RM (1981) Changes in herbaceous and suffrutescent perennials in grazed and ungrazed desertified grassland in southeastern Arizona. *The American Midland Naturalist*, **108**, 159–169.
- Christensen EM, Welsh SL (1963) Presettlement vegetation of the valleys of western Summit and Wasatch counties, Utah. *Proceedings of the Utah Academy*, **40**, 163–174.
- Clarke SE, Tisdale EW, Skoglund NA (1943) *The Effects of Climate and Grazing Practices on Short-grass Prairie Vegetation in Southern Alberta and Southwestern Saskatchewan*. Publication No. 46, Canadian Dominion, Department of Agriculture, Ottawa.
- Dix RL (1959) The influence of grazing on the thin-soil prairies of Wisconsin. *Ecology*, **40**, 36–49.
- Duvell VI, Linnartz NE (1967) Influences of grazing and fire on vegetation and soil of longleaf pine-bluestem range. *Journal of Range Management*, **20**, 241–247.
- Evanko AB, Peterson RA (1955) Comparisons of protected and grazed mountain rangelands in southwestern Montana. *Ecology*, **36**, 71–82.
- Frank AB, Tanaka DL, Hofmann L, *et al.* (1995) Soil carbon and nitrogen of northern great plains grasslands as influenced by long-term grazing. *Journal of Range Management*, **48**, 470–474.
- Gardner JL (1950) Effects of thirty years of protection from grazing in the desert grassland. *Ecology*, **30**, 44–50.
- Gardner JL (1951) Vegetation of the creosotebush area of the Rio Grande valley in New Mexico. *Ecological Monographs*, **21**, 379–403.
- Gillen RL, McCollum FT, Hodges ME, *et al.* (1991) Plant community responses to short duration grazing in tall-grass prairie. *Journal of Range Management*, **44**, 124–128.
- Hartnett DC, Hickmen KR, Fischer Walter LE (1996) Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. *Journal of Range Management*, **49**, 413–420.
- Heitschmidt RK, Dowhower SL, Gordon RA, *et al.* (1985) *Response of Vegetation to Livestock Grazing at The Texas Experimental Ranch*. Report B-1515. November 1985, Texas Agricultural Experiment Station, Texas.
- Henry GHR (1998) Environmental influences on the structure of sedge meadows in the Canadian High Arctic. *Plant Ecology*, **134**, 119–129.
- Holechek JL, Stephenson T (1983) Comparison of big sagebrush vegetation in northcentral New Mexico under moderately grazed and grazing excluded conditions. *Journal of Range Management*, **36**, 455–456.
- Holmgren RC, Hutchings SS (1971) *Salt Desert Shrub Response to Grazing Use. Wildland Shrubs – their Biology and Utilization*. General Technical Report INT-I, 1972, USDA Forest Service.
- Hutchings SS, Stewart G (1953) *Increasing Forage yields and Sheep Production on Intermountain Winter Ranges*. Circular 925, USDA.
- Johnson WM (1956) The effect of grazing intensity on plant composition, vigor, and growth of pine-bunchgrass ranges in central Colorado. *Ecology*, **37**, 790–798.
- Kelting RW (1954) Effects of moderate grazing on the composition and plant production of a native tall-grass prairie in central Oklahoma. *Ecology*, **35**, 200–207.
- Kerley GIH, Whitford WG (2000) Impact of grazing and desertification in the Chihuahuan desert: plant communities, granivores and granivory. *The American Midland Naturalist*, **144**, 78–91.
- Kipple GE, Costello DF (1960) *Vegetation and Cattle Responses to different Intensities of Grazing on Short-grass Ranges on the Central Great Plains*. Bulletin No. 1216, pp. 82, US Dept. Agric. Tech., Washington, DC.
- Launchbaugh JL (1955) Vegetational changes in the San Antonio prairie associated with grazing, retirement from grazing, and abandonment from cultivation. *Ecological Monographs*, **25**, 39–57.
- Laycock WA (1967) How heavy grazing protection affects sagebrush-grass ranges. *Journal of Range Management*, **20**, 206–213.
- Laycock WA, Conrad PW (1981) Responses of vegetation and cattle to various systems of grazing on seeded and native mountain rangelands in eastern Utah. *Journal of Range Management*, **34**, 52–58.
- Lewis CE, Tanner GW, Terry WS (1988) Plant responses to pine management and deferred-rotation grazing in north Florida. *Journal of Range Management*, **41**, 460–465.
- McPherson GR, Wright HA (1990) Effects of cattle grazing and *Juniperus pinchotii* canopy cover and production in western Texas. *The American Midland Naturalist*, **123**, 144–151.
- Milchunas DG, Lauenroth WK, Burke IC (1998) Livestock grazing: animal and plant biodiversity of short-grass steppe and the relationship to ecosystem function. *Oikos*, **83**, 65–74.
- Milchunas DG, Lauenroth WK, Chapman PL (1992) Plant competition, abiotic, and long-and short-term effects of large herbivores on demography of opportunistic species in a semiarid grassland. *Oecologia*, **92**, 520–531.

- Milchunas DG, Lauenroth WK, Chapman PL, *et al.* (1989) Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. *Vegetatio*, **80**, 11–23.
- Milchunas DG, Lauenroth WK, Chapman PL, *et al.* (1990) Community attributes along a perturbation gradient in a shortgrass steppe. *Journal of Vegetation Science*, **1**, 375–384.
- Naeth MA, Chanasyk DS, Rothwell RL, *et al.* (1991) Grazing impacts on soil water in mixed prairie and fescue grassland ecosystems in Alberta. *Canadian Journal of Soil Science*, **71**, 312–325.
- Neiland BM, Curtis JT (1956) Differential responses to clipping of six prairie grasses in Wisconsin. *Ecology*, **37**, 355–365.
- Pearson HA, Whitaker LB (1974) Yearlong grazing of slash pine ranges: effects on herbage and browse. *Journal of Range Management*, **27**, 195–197.
- Pearson LC (1965) Primary production in grazed and ungrazed desert communities of eastern Idaho. *Ecology*, **46**, 278–285.
- Pfeiffer KE, Steuter AA (1994) Preliminary response of sandhills prairie to fire and bison grazing. *Journal of Range Management*, **47**, 395–397.
- Pickford GD (1932) The influence of continued heavy grazing and of promiscuous burning on spring-fall ranges in Utah. *Ecology*, **13**, 159–171.
- Pieper RD (1968) Comparison of vegetation on grazed and ungrazed pinyon-juniper grassland sites in southcentral New Mexico. *Journal of Range Management*, **21**, 51–52.
- Rasmussen LL, Brotherson JD (1986) Response of winterfat (*Ceratoides lanata*) communities to release from grazing pressure. *Great Basin Naturalist*, **46**, 148–156.
- Rauzi F (1963) Water intake and plant composition as affected by differential grazing on rangeland. *Journal of Soil and Water Conservation*, **18**, 114–116.
- Rebollo S, Milchunas DG, Noy-Meir I, *et al.* (2002) The role of a spiny plant refuge in structuring grazed shortgrass steppe plant communities. *Oikos*, **98**, 53–64.
- Roundy BA, Jordan GI (1998) Vegetational changes in relation to livestock exclusion and rootplowing in southeastern Arizona. *The Southwestern Naturalist*, **33**, 425–436.
- Schulz TT, Leininger WC (1989) *Differences in Riparian Vegetation Structure Between Grazed Areas and Exlosures*. Colorado Agriculture Experiment Station and the USDA Rangeland Research Grants Program.
- Schuster JL (1964) Root development of native plants under three grazing intensities. *Ecology*, **45**, 63–70.
- Smith DA, Schmutz EM (1975) Vegetative changes on protected vs. grazed desert grassland ranges in Arizona. *Journal of Range Management*, **28**, 453–458.
- Smith DR (1967) *Effects of Cattle Grazing on a Ponderosa Pine-bunchgrass Range in Colorado*. Bulletin No. 1371, USDA Technical Bulletin.
- Smoliak S, Dormaar JF, Johnston A (1972) Long-term grazing effects on *Stipa-Bouteloua* prairie soils. *Journal of Range Management*, **25**, 246–250.
- Smoliak SJF (1974) Range vegetation and sheep production at three stocking rates on *Stipa-Bouteloua* prairie. *Journal of Range Management*, **27**, 23–26.
- Sneva FA, Rittenhouse LR, Tueller TE, *et al.* (1984) *Changes in Protected and Grazed Sagebrush-grass in Eastern Oregon. 1937 to 1974*. Agricultural Experiment Station Oregon State University, Corvallis.
- Tomanek GW, Albertson FW (1953) Some effects of different intensities of grazing on mixed prairies near Hayes, Kansas. *Journal of Range Management*, **6**, 299–306.
- Tomanek GW, Albertson FW (1957) Variations in cover, composition, production and roots of vegetation on two prairies in western Kansas. *Ecological Monographs*, **27**, 267–281.
- Truscott DR, Currie PO (1989) Cattle preference for a hybrid grass: chemical and morphological relationships. *Journal of Range Management*, **42**, 22–27.
- Valone TJ, Kelt DA (1999) Fire and grazing in a shrub-invaded arid grassland community: independent or interactive ecological effects? *Journal of Arid Environments*, **42**, 15–28.
- Vogel WG, VanDyne GM (1966) Vegetation responses to grazing management on a foothill sheep range. *Journal of Range Management*, **19**, 80–85.
- Whisenant SG, Wagstaff FJ (1991) Successional trajectories of a grazed salt desert shrubland. *Vegetatio*, **94**, 133–140.
- Willms WD, Smoliak S, Dormaar JF (1985) Effects of stocking rate on a rough fescue grassland vegetation. *Journal of Range Management*, **38**, 220–225.
- Zimmerman GT, Neuenschwander LF (1984) Livestock grazing influences on community structure, fire intensity, and fire frequency within the Douglas fir/ninebark habitat type. *Journal of Range Management*, **37**, 104–110.

Northern and Central Europe

- Bakker JP (1978) Some experiments on heathland conservation and regeneration. *Phytocoenosis*, **7**, 351–370.
- Bakker JP (1987) Restoration of species-rich grassland after a period of fertilizer application. In: *Disturbance in Grasslands* (eds van Andel J, Bakker JP, Snaydon RW), pp. 185–200. Dr. W Junk, Dordrecht.
- Bakker JP, de Bie S, Dallinga JH, *et al.* (1983) Sheep-grazing as a management tool for heathland conservation and regeneration in the Netherlands. *Journal of Applied Ecology*, **20**, 541–560.

- Bakker JP, Dekker M, de Vries Y (1980) The effect of different management practices on a grassland community and the resulting fate of seedlings. *Acta Botanica Neerlandica*, **29**, 469–482.
- Bakker JP, Leeuw JD, Wieren SEV (1983) Micro-patterns in grassland vegetation created and sustained by sheep-grazing. *Vegetatio*, **55**, 153–161.
- Bullock JM, Hill CB, Dale MP, *et al.* (1994) An experimental study of the effects of sheep grazing on vegetation change in a species-poor grassland and the role of seedling recruitment into gaps. *Journal of Applied Ecology*, **31**, 493–507.
- Bullock JM, Hill CB, Silvertown J, *et al.* (1995) Gap colonization as a source of grassland community change: effects of gap size and grazing on the rate and mode of colonization by different species. *Oikos*, **72**, 273–282.
- Gibson CWD, Brown VK (1991) The nature and rate of development of calcareous grassland in southern Britain. *Biological Conservation*, **58**, 297–316.
- Gibson CWD, Brown VK (1992) Grazing and vegetation change – deflected or modified succession. *Journal of Applied Ecology*, **29**, 120–131.
- Grime JP (1990) Mechanisms promoting floristic diversity in calcareous grasslands. In: *Calcareous Grasslands – Ecology and Management* (eds Hillier SH, Walton DWH, Wells DA), pp. 51–56. Bluntisham Books, Huntington.
- Helle T, Aspi J (1983) Effects of winter grazing by reindeer on vegetation. *Oikos*, **40**, 337–343.
- Hill MO, Evans DF, Bell, SA (1992) Long-term effects of excluding sheep from hill pastures in North Wales. *Journal of Ecology*, **80**, 1–13.
- Hulme P, Pakeman R, Torwell L, *et al.* (1999) The effects of controlled sheep grazing on the dynamics of upland *Agrostis-Festuca* grassland. *Journal of Applied Ecology*, **36**, 886–900.
- Hunter RF (1962) Hill sheep and their pasture: a study of sheep-grazing in southeast Scotland. *Journal of Ecology*, **50**, 651–680.
- Jutila H (1999) Effect of grazing on the vegetation of shore meadows along the Bothnian Sea, Finland. *Plant Ecology*, **140**, 77–88.
- Ljung E (1970) *Arbtytet omkring fållor och fårhus på Ölands Stora Alvar*. Bachelor thesis, Uppsala University, Uppsala.
- Moen J, Oksanen L (1998) Long-term exclusion of folivorous mammals in two arctic-alpine plant communities: a test of the hypothesis of exploitation. *Oikos*, **82**, 333–346.
- Oksanen L, Moen J (1994) Species-specific plant responses to exclusion of grazers in three Fennoscandian tundra habitats. *Ecoscience*, **1**, 31–39.
- Rawes M (1981) Further results of excluding sheep from high-level grasslands in the North Pennines. *Journal of Ecology*, **69**, 651–670.
- Schläpfer M, Zoller H, Körner C (1998) Influences of mowing and grazing on plant species composition in calcareous grassland. *Botanica Helvetica*, **108**, 57–67.
- Thorsteinsson I (1986) The effect of grazing on stability and development of northern rangelands: a case of Iceland. In: *Grazing Research at Northern Latitudes* (ed. Gudmundsson O), pp. 37–43. Plenum, New York.
- Titlyanova A, Rusch G, van der Maarel E (1988) Biomass structure of limestone grasslands on Öland in relation to grazing intensity. *Acta Phytogeographica Suecica*, **76**, 125–134.
- van den Bos J, Bakker JP (1990) The development of vegetation patterns by cattle grazing at low stocking density in the Netherlands. *Biological Conservation*, **51**, 263–272.
- Vorontzova LI, Zaugolnova LB (1985) Population biology of steppe plants. In: *The Population Structure of Vegetation* (ed. White J), pp. 143–178. Dr. W Junk, Dordrecht.
- Ward LK (1990) Management of grasslands – scrub mosaics. In: *Calcareous Grasslands – Ecology and Management* (eds Hillier SH, Walton DWH, Wells DA), pp. 134–139. Bluntisham Books, Huntington.
- Wegener C, Odasz-Albrigtsen AM (1998) Do svalbard reindeer regulate standing crop in the absence of predators? A test of the ‘exploitation ecosystems’ model. *Oecologia*, **116**, 202–206.
- Welch D (1984) Studies in the grazing of heather moorland in North-east Scotland. I. Site descriptions and patterns of utilization. *Journal of Applied Ecology*, **21**, 179–195.
- Welch D (1986) Studies in the grazing of heather moorland in North-east Scotland. V. Trends in *Nardus stricta* and other unpalatable graminoids. *Journal of Applied Ecology*, **23**, 1047–1058.
- Wiegolaski FE (1975) Comparison of plant structure on grazed and ungrazed tundra meadows. In: *Fennoscandian Tundra Ecosystems* (ed. Wiegolaski FE). Springer-Verlag, Berlin.
- Willems JH (1990) Calcareous grasslands in continental Europe. In: *Calcareous Grasslands – Ecology and Management* (eds Hillier SH, Walton DWH, Wells DA), pp. 3–10. Bluntisham Books, Huntington.

South America

- Adler PB, Morales JM (1999) Influence of environmental factors and sheep grazing on an Andean grassland. *Journal of Range Management*, **52**, 471–481.
- Aguiar M, Sala OE (1998) Interactions among grasses, shrubs and herbivores in Patagonian grass-shrubs steppes. *Ecología Austral*, **8**, 201–210.
- Altesor A, Pezzani F, Grun S, *et al.* (1999) Relationships between spatial strategies and morphological attri-

- butes in an Uruguayan grassland: a functional approach. *Journal of Vegetation Science*, **10**, 457.
- Beeskow AM, Elissalde NO, Rostagno CM (1995) Ecosystem changes associated with grazing intensity on the Punta Ninfas rangelands of Patagonia, Argentina. *Journal of Range Management*, **48**, 517–522.
- Bertiller MB (1996) Grazing effects on sustainable semi-arid rangelands in Patagonia: the state and dynamics of the soil seed bank. *Environmental Management*, **20**, 123–132.
- Bisigato AJ, Bertiller MB (1997) Grazing effect on patchy dryland vegetation in northern Patagonia. *Journal of Arid Environments*, **36**, 639–653.
- Boldrini II, Eggers L (1996) Vegetação campestre do sul do Brasil: dinâmica de espécies à exclusão do gado. *Acta Botânica Brasileira*, **10**, 37–50.
- Boldrini II, Eggers L (1997) Directionality of succession after grazing exclusion in grassland in the south of Brazil. *Coenoses*, **12**, 63–66.
- Chaneton EJ, Lemcoff JH, Lavado RS (1996) Nitrogen and phosphorus cycling in grazed and ungrazed plots in a temperate subhumid grassland in Argentina. *Journal of Applied Ecology*, **33**, 291–302.
- Cingolani A (1999) *Efectos de 100 años de pastoreo ovino sobre la vegetación y suelos del norte de Tierra del Fuego*. PhD Thesis, Department of Biological Sciences, Buenos Aires University, Argentina.
- Collantes MB, Anchorena J (1993) Las malezas exóticas y plantas escapadas de cultivo en la región de estepa de Tierra del Fuego. *Parodiana*, **8**, 213–217.
- Collantes MB, Anchorena J, Koremblit G (1989) A soil gradient in Magellanic *Empetrum* heathland. *Vegetatio*, **80**, 183–193.
- Díaz S, Acosta A, Cabido M (1992) Morphological analysis of herbaceous communities under different grazing regimes. *Journal of Vegetation Science*, **3**, 689–696.
- Díaz S, Acosta A, Cabido M (1994) Community structure in montane grasslands of central Argentina in relation to land use. *Journal of Vegetation Science*, **5**, 483–488.
- Díaz S, Acosta A, Cabido M (1994) Grazing and the phenology of flowering and fruiting in a montane grassland in Argentina: a niche approach. *Oikos*, **70**, 287–295.
- Díaz S, Noy-Meir I, Cabido M (2001) Can grazing response of herbaceous plants be predicted from simple vegetative traits? *Journal of Applied Ecology*, **38**, 497–508.
- Distel RA, Klich MG (1995) Vegetative and reproductive characteristics in two *Stipa* species differing in grazing tolerance. In: *Proceedings of the 5th International Rangeland Congress*, Salt Lake City, Utah, pp. 119–120.
- Gonnet JM (1998) *Influencia del pastoreo sobre poblaciones de aves y mamíferos herbívoros en la región de la Reserva de la Biosfera 'Ñacuñán', Mendoza, Argentina*. PhD Thesis, National University of Córdoba, Argentina.
- Grünwaldt EG, Pedrani AR, Vich AI (1994) Goat grazing in the arid piedmont of Argentina. *Small Ruminant Research*, **13**, 211–216.
- Hidalgo LG, Cahuepé MA (1991) Effects of seasonal rest in aboveground biomass for a native grassland of the flood pampa, Argentina. *Journal of Range Management*, **44**, 471–474.
- León RJC, Aguiar M (1985) El deterioro por uso pasturil en estepas herbáceas patagónicas. *Phytocoenologia*, **13**, 181–196.
- Llorens EM (1995) Viewpoint: the state and transition model applied to the herbaceous layer of Argentina's calden forest. *Journal of Range Management*, **48**, 442–447.
- Oosterheld M, Sala OE (1990) Effects of grazing on seedling establishment: the role of seed and safe-site availability. *Journal of Vegetation Science*, **1**, 353–358.
- Perelman SB, León RJC, Bussacca JP (1997) Floristic changes related to grazing intensity in Patagonian shrub steppe. *Ecography*, **20**, 400–406.
- Posse G, Anchorena J, Collantes MB (2000) Spatial micro-patterns in the steppe of Tierra del Fuego induced by sheep grazing. *Journal of Vegetation Science*, **11**, 43–50.
- Pucheta E, Díaz S, Cabido M (1992) The effect of grazing on the structure of a high plateau grassland in central Argentina. *Coenoses*, **7**, 145–152.
- Pucheta E, Vendramini F, Cabido M, *et al.* (1998) Estructura y funcionamiento de un pastizal de montaña bajo pastoreo y su respuesta luego de su exclusión. *Revista de la Facultad de Agronomía de La Plata*, **103**, 77–92.
- Rosati VR, Bucher EH (1995) Relative abundance and diet composition of Chacoan caviés in relation to range condition. *Journal of Range Management*, **48**, 482–486.
- Rusch GM, Oosterheld M (1997) Relationship between productivity, and species and functional group diversity in grazed and non-grazed pampas grassland. *Oikos*, **78**, 519–526.
- Sala OE, Oosterheld M, León RJC, *et al.* (1986) Grazing effects upon plant community structure in subhumid grasslands of Argentina. *Vegetatio*, **67**, 27–32.
- San José JJ, Fariñas MR (1991) Temporal changes in the structure of a *Trachypogon* savanna protected for 25 years. *Acta Oecologica*, **12**, 237–247.

Appendix B

Proforma utilized in data gathering, standardization and codification.

Region: Africa, Australasia, Central Asia, Mediterranean, North America, Northern and Central Europe, South America.

Latitude and longitude

Latitudinal category: tropical, temperate, austral, boreal. Tropical-temperate boundary, 25°; temperate-boreal, 60°; temperate-austral, 45°.

Annual precipitation (mm)

Precipitation category according to Köppen (1918): Dry, humid.

Seasonality of rainfall: summer, winter, rainfall evenly distributed throughout the year.

Evolutionary history of herbivory

Long history: continuous occupation by ungulates and/or similar large (>25 kg) mammalian herbivores since at least the Pleistocene (ca. 10 000 years ago), including the presence of domestic or semidomestic ungulates since at least ca. 4000 years ago (e.g. Africa, Mediterranean, Andean South America), and the presence of wild herbivores (e.g. North America east of the Rocky Mountains, non-Andean South America).

Short history: wild ungulates absent since before the Pleistocene; or their presence discontinued in the Pleistocene; occupation by large (wild or domestic) mammalian herbivores occurred for the first time less than 4000 years ago (e.g. Australasia, North America west of the Rockies).

Soil type: sandy, clayey, gravelly, loamy, organic.

Soil nutrient content: nitrogen and phosphorus content.

Productivity: aboveground net primary productivity or standing biomass.

Stocking rate: number of animals per ha.

% consumption: what proportion of the ANPP is consumed by the herbivores.

Grazing frequency: frequency and duration of grazing at the site.

Grazing pressure: no grazing; light/moderate (selective); heavy (mostly nonselective).

Type of grazer: cattle, goats, Camelidae, etc.

Response variable: variable on which the effects of grazing are measured (e.g. cover of annual vs. perennial plants, richness of prostrate vs. erect species).

Response direction: increase (+) or a decrease (−) in the response variable in the face of grazing.

Response mean: % change of the mean as a response of grazing (e.g. grazing is associated with 20% reduction of plant height).

Response variance: variance (or other estimator of dispersion, such as standard deviation or standard error) for the response variable.

P-value: corresponding to test performed to assess differences in response value as a result of grazing.

Degrees of freedom: Corresponding to test performed to assess differences in response value as a result of grazing.

Appendix C

Contingency tables. The values in the response columns correspond to relative frequency of observations documenting a negative (−), neutral (0) or positive (+) response to grazing of the abundance or richness of plants bearing the attribute listed in each row (with 100% being N, or the total number of observations in each contingency table). *P* corresponds to the Cochran–Mantel–Haenszel Association test (CMH) in the case of comparisons involving all sites (and controlling for precipitation and grazing history), and to the Likelihood Ratio χ^2 test (G^2) in the case of comparisons, which involve particular categories of precipitation and/or evolutionary history of grazing. In both CMH and G^2 tests, the null hypothesis was that the direction of response to grazing was not associated with a specific trait. Rejection of the null hypothesis meant that plant species with some attributes were more abundant or more common than plants with other attributes within the trait. Being unable to reject the null hypothesis meant that directions of response to grazing were not significantly different between the trait attributes. In all cases df, (number of possible grazing responses −1) × (number of attributes in a trait −1); the degrees of freedom are the same for the comparisons involving all sites or individual combinations corresponding to each trait, NC, not computable, either because there were too few observations or the sum of one or more rows or columns in the table was zero. Table A1

Table A1

	Response					
	<i>N</i>	(-)	(0)	(+)	<i>P</i>	df
<i>Life History – abundance</i>						
All Sites	130				< .0.0001	2
Annual		5.38	20.77	33.85		
Perennial		19.23	14.62	6.15		
Dry	78				0.005	
Annual		5.13	26.92	24.36		
Perennial		15.38	20.51	7.69		
Humid	52				< .0.0001	
Annual		5.77	11.54	48.08		
Perennial		25	5.77	3.85		
Short history	63				< .0.0001	
Annual		1.59	19.05	36.51		
Perennial		22.22	14.29	6.35		
Long History	67				0.004	
Annual		8.96	22.39	31.34		
Perennial		16.42	14.93	5.97		
Dry + short History	44				0.006	
Annual		2.27	22.73	27.27		
Perennial		18.18	20.45	9.09		
Dry + long history	34				0.353	
Annual		8.82	32.35	20.59		
Perennial		11.76	20.59	5.88		
Humid + short history	19				< .0.0001	
Annual		0	10.53	57.89		
Perennial		31.58	0	0		
Humid + long history	33				0.009	
Annual		9.09	12.12	42.42		
Perennial		21.21	9.09	6.06		
<i>Life History – spp. Richness</i>						
All sites	65				0.019	2
Annual		11.94	8.96	34.33		
Perennial		22.39	10.45	11.94		
Dry	12				0.002	
Annual		0	8.33	41.67		
Perennial		33.33	16.67	0		
Humid	53				0.169	
Annual		13.21	9.43	33.96		
Perennial		18.87	9.43	15.09		
Short history	26				0.009	
Annual		3.85	11.54	42.31		
Perennial		19.23	15.38	7.69		
Long history	41				0.309	
Annual		17.07	7.32	29.27		
Perennial		24.39	7.32	14.63		
Dry + short history	5				NC	
Dry + long history	7				NC	
Humid + short history	21				0.038	
Annual		4.76	9.52	47.62		
Perennial		19.05	9.52	9.52		
Humid + long history	32				0.922	
Annual		18.75	9.38	25		
Perennial		18.75	9.38	18.75		

(contd.)

Table A1. (Contd.)

	Response					
	<i>N</i>	(−)	(0)	(+)	<i>P</i>	<i>df</i>
<i>Canopy Height – abundance</i>						
All Sites	180				<0.0001	2
Short		5.56	19.44	32.78		
Tall		24.44	13.33	4.44		
Dry	62				0.008	
Short		11.29	16.13	27.42		
Tall		25.81	9.68	9.68		
Humid	118				<.0.0001	
Short		2.54	21.19	35.59		
Tall		23.73	15.25	1.69		
Short history	31				0.05	
Short		9.68	16.13	32.26		
Tall		19.35	16.13	6.45		
Long history	149				<.0.0001	
Short		4.7	20.13	32.89		
Tall		25.5	12.75	4.03		
Dry + short history	12				0.785	
Short		25	16.67	8.33		
Tall		33.33	8.33	8.33		
Dry + long history	50				0.006	
Short		8	16	32		
Tall		24	10	10		
Humid + short history	19				0.011	
Short		0	15.79	47.37		
Tall		10.53	21.05	5.26		
Humid + long history	99				<.0.0001	
Short		3.03	22.22	33.33		
Tall		26.26	14.14	1.01		
<i>HABIT – abundance</i>						
All Sites	37				<.0.0001	2
Erect		29.73	2.7	5.41		
Prostrate		0	8.11	54.05		
Dry	6				0.088	
Erect		16.67	16.67	0		
Prostrate		0	16.67	50		
Humid	31				<.0.0001	
Erect		32.26	0	6.45		
Prostrate		0	6.45	54.84		
Short history	10				0.005	
Erect		30	10	0		
Prostrate		0	10	50		
Long History	27				<.0.0001	
Erect		29.63	0	7.41		
Prostrate		0	7.41	55.56		
Dry + Short History	5				0.138	
Erect		20	20	0		
Prostrate		0	20	40		
Dry + Long History	1				NC	
Humid + Short History	5				<.0.0001	
Erect		40	0	0		
Prostrate		0	0	60		
Humid + long history	26				<.0.0001	
Erect		30.77	0	7.69		

(contd.)

Table A1. (Contd.)

	N	Response			P	df
		(-)	(0)	(+)		
Prostrate		0	7.69	53.85		
<i>Architecture – abundance</i>						
All sites	71				0.002	6
Leafy stem		5.63	2.82	8.45		
Rosette		4.23	2.82	26.76		
Stoloniferous		4.23	2.82	15.49		
Tussock		19.72	2.82	4.23		
Dry	27				0.032	
Leafy stem		0	7.41	14.81		
Rosette		0	7.41	3.7		
Stoloniferous		11.11	7.41	11.11		
Tussock		25.93	3.7	7.41		
Humid	44				<0.001	
Leafy stem		9.09	0	4.55		
Rosette		6.82	0	40.91		
Stoloniferous		0	0	18.18		
Tussock		15.91	2.27	2.27		
Short history	22				0.040	
Leafy stem		9.09	9.09	18.18		
Rosette		0	9.09	9.09		
Stoloniferous		0	0	22.73		
Tussock		13.64	0	9.09		
Long history	49				<0.001	
Leafy stem		4.08	0	4.08		
Rosette		6.12	0	34.70		
Stoloniferous		6.12	4.08	12.24		
Tussock		22.45	4.08	2.04		
Dry + short history	15				0.006	
Leafy stem		0	13.33	26.67		
Rosette		0	13.33	0		
Stoloniferous		0	0	20		
Tussock		20	0	6.67		
Dry + long history	12				NC	
Humid + short history	7				NC	
Humid + long history	37				<0.001	
Leafy stem		5.41	0	5.41		
Rosette		8.11	0	43.24		
Stoloniferous		0	0	16.22		
Tussock		18.92	2.7	0		
<i>Architecture – graminoids only, abundance</i>						
All sites	35				0.002	
Stoloniferous		8.57	5.71	31.43		
Tussock		40.00	5.71	8.57		
Dry	18				0.374	
Stoloniferous		16.67	11.11	16.67		
Tussock		38.89	5.56	11.11		
Humid	17				<0.001	
Stoloniferous		0	0	47.06		
Tussock		41.18	5.88	5.88		
Short history	10				NC	
Long history	25				0.014	
Stoloniferous		12.00	8.00	24.00		
Tussock		44.00	8.00	4		

(contd.)

Table A1. (Contd.)

	Response				P	df
	N	(-)	(0)	(+)		
Dry + short history	7				NC	
Dry + long history	11				0.411	
Stoloniferous		27.27	18.18	0		
Tussock		36.36	9.09	9.09		
Humid + short history	3				NC	
Humid + long history	14				<0.0001	
Stoloniferous		0	0	42.86		
Tussock		50.00	7.14	0		
<i>Architecture – forbs only, abundance</i>						
All sites	36				0.204	
Rosette		8.33	5.56	52.78		
leafy stem		11.11	5.56	16.67		
Dry	9				NC	
Humid	27				NC	
Short history	12				0.351	
Rosette		0	16.67	16.67		
Leafy stem		16.67	16.67	33.33		
Long history	24				NC	
Dry + short history	8				NC	
Dry + long history	1				NC	
Humid + short history	4				NC	
Humid + long history	23				NC	
<i>Growth form – abundance</i>						
All Sites	341				<0.0001	6
Forb		4.4	18.48	9.09		
Graminoid		14.66	16.13	6.74		
Herbaceous legume		1.76	0.59	2.93		
Woody		6.16	12.32	6.74		
Dry	200				<0.0001	
Forb		3.5	19	7		
Graminoid		15.5	21	4		
Herbaceous legume		1.5	0	2		
Woody		4	15.5	7		
Humid	141				0.048	
Forb		5.67	17.73	12.06		
Graminoid		13.48	9.22	10.64		
Herbaceous legume		2.13	1.42	4.26		
Woody		9.22	7.8	6.38		
Short history	120				0.180	
Forb		3.33	21.67	5.83		
Graminoid		6.67	28.33	4.17		
Herbaceous legume		1.67	0.83	1.67		
Woody		4.17	20	1.67		
Long history	221				<0.0001	
Forb		4.98	16.74	10.86		
Graminoid		19	9.5	8.14		
Herbaceous legume		1.81	0.45	3.62		
Woody		7.24	8.14	9.5		
Dry + short history	81				0.016	
Forb		1.23	27.16	2.47		
Graminoid		6.17	37.04	0		
Herbaceous legume		0	0	1.23		
Woody		0	22.22	2.47		

(contd.)

Table A1. (Contd.)

	N	Response			P	df
		(-)	(0)	(+)		
Dry + long history	119				0.002	
Forb		5.04	13.45	10.08		
Graminoid		21.85	10.08	6.72		
Herbaceous legume		2.52	0	2.52		
Woody		6.72	10.92	10.09		
Humid + short history	39				0.130	
Forb		7.69	10.26	12.82		
Graminoid		7.69	10.26	12.82		
Herbaceous legume		5.13	2.56	2.56		
Woody		12.82	15.38	0		
Humid + long history	102				0.007	
Forb		4.9	20.59	11.76		
Graminoid		15.69	8.82	9.8		
Herbaceous legume		0.98	0.98	4.9		
Woody		7.84	4.9	8.82		
<i>Growth form – spp. richness</i>						
All sites	64				0.094	6
Forb		10.94	14.06	15.63		
Graminoid		17.19	20.31	3.13		
Herbaceous legume		0	0	1.56		
Woody		6.25	6.25	4.69		
Dry	19				NC	
Humid	45				0.056	
Forb		8.89	15.56	15.56		
Graminoid		15.56	24.44	4.44		
Herbaceous legume		0	0	2.22		
Woody		8.89	4.44	0		
Short history	22				NC	
Long History	42				0.002	
Forb		9.52	16.67	16.67		
Graminoid		16.67	26.19	0		
Herbaceous legume		0	0	2.38		
Woody		4.76	0	7.14		
Dry + short history	6				NC	
Dry + long history	13				NC	
Humid + short history	16				NC	
Humid + long history	29				0.007	
Forb		3.45	24.14	13.79		
Graminoid		10.34	37.93	0		
Herbaceous legume		0	0	3.45		
Woody		6.9	0	0		
<i>Palatability – abundance</i>						
All sites	52				0.005	2
Palatable		28.85	13.46	5.78		
Unpalatable		11.54	13.46	26.93		
Dry	29				<.0.0001	
Palatable		24.14	24.14	0		
UnPalatable		0	20.69	31.03		
Humid	23				0.344	
Palatable		34.78	0	13.04		
Unpalatable		26.09	4.35	21.74		
Short history	8				0.062	
Palatable		25	25	0		

(contd.)

Table A1. (Contd.)

	Response				P	df
	N	(-)	(0)	(+)		
Unpalatable		0	25	25		
Long History	44				0.015	
Palatable		29.55	11.36	6.82		
Unpalatable		13.64	11.36	27.27		
Dry + short history	8				0.062	
Palatable		25	25	0		
Unpalatable		0	25	25		
Dry + long history	21				<0.001	
Palatable		23.81	23.81	0		
Unpalatable		0	19.05	33.33		
Humid + short history	0				NC	
Humid + long history	23				0.344	
Palatable		34.78	0	13.04		
Unpalatable		26.09	4.35	21.74		
<i>Origin – abundance</i>						
All sites	22				0.156	2
Exotic		8.7	21.74	47.83		
Native		17.39	4.35	0		
Dry	8				NC	
Humid	14				0.016	
Exotic		7.14	28.57	28.57		
Native		28.57	7.14	0		
Short history	14				0.013	
Exotic		7.14	21.43	35.71		
Native		28.57	7.14	0		
Long history	8				NC	
Dry + short history	3				NC	
Dry + long history	5				NC	
Humid + short history	10				0.080	
Exotic		10	20	20		
Native		40	10	0		
Humid + long history	4				NC	
<i>Origin – spp. richness</i>						
All sites	48				0.524	2
Exotic		6.12	28.57	22.45		
Native		8.16	22.45	12.24		
Dry	2				NC	
Humid	46				0.470	
Exotic		4.35	28.26	21.74		
Native		8.7	23.91	13.04		
Short history	43				0.522	
Exotic		4.65	30.23	18.6		
Native		9.3	25.58	11.63		
Long history	5				NC	
Dry + short history	0				NC	
Dry + long history	2				NC	
Humid + short history	43				0.513	
Exotic		4.65	30.23	18.6		
Native		9.3	25.58	11.63		
Humid + long history	3				NC	