

Simple traits do not predict grazing response in Australian dry shrublands and woodlands

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Summary

1. Plant species composition and species response to grazing are fundamental to the management of grazing lands. Reliable prediction of grazing responses from species' traits would be a major step forward in generalizing knowledge and management beyond the locality. Recently results have been presented showing that plant species' responses to grazing in subhumid grasslands in Argentina and Israel could be predicted from simple traits: height, leaf size, life history and specific leaf area (SLA). This study assessed whether those relationships between traits and grazing responses hold for Australian semi-arid and arid shrublands and woodlands.

2. Eleven lists of grazing responses from five published grazing studies were matched with a plant trait data set. Trait distributions were compared between response groups pooled across studies. Relationships between traits and grazing response were also assessed, both within and across studies, using meta-analysis.

3. Overall there was little evidence for predictability of grazing responses with simple traits in the semi-arid and arid shrublands and woodlands. There were relationships between grazing response and life history and growth form, and some weak evidence for grazing increasers having high SLA.

4. *Synthesis and applications.* It was concluded that prediction of grazing responses with simple traits is less clear in semi-arid and arid rangelands, which are characterized by openness at ground level and high diversity of growth forms, compared with sub-humid grasslands that have structurally simple, continuous swards. The finding that species' traits may have differing predictive capacity for grazing responses in different situations means that we need more empirical studies in different situations. The most important contrasts between situations for investigation are likely to be on axes of rainfall/productivity and evolutionary history of grazing.

Key-words: ecological generalization, height, life history, plant functional types, range condition, seed mass, SLA, vegetation change.

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Introduction

Plant species composition and response to grazing are central to management of grazing lands (Stoddart, Smith & Box 1975; Morton *et al.* 1995). Determining species' responses to grazing at a location is an essential step, but unless simple traits can be identified to predict those responses the results cannot be generalized beyond the locality to other sets of species (Landsberg, Lavorel & Stol 1999; McIntyre *et al.* 1999).

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Recently, Díaz, Noy-Meir & Cabido (2001) demonstrated that grazing responses could be predicted from simple measurable traits of herbaceous plant species from subhumid Argentine and Israeli grasslands (Argentina, *c.* 880 mm mean annual rainfall, *c.* 10 °C mean annual temperature; Israel, *c.* 500 mm mean annual rainfall, 21 °C mean annual temperature). This is a major step because it suggests that at a new site with different species, grazing responses could be predicted by measuring traits of plants rather than by carrying out a new grazing trial. This could potentially save significant research effort and better direct management. The critical assumption is that the relationships between species' traits and species' responses to grazing hold in the new site. One way that this assumption could fail would be for species to respond inconsistently to grazing

(Noy-Meir, Gutman & Kaplan 1989; Vesik & Westoby 2001); another would be if the relationships between traits and responses were context-specific. This second possibility was the objective of the present study: to test if the relationships identified by Díaz, Noy-Meir & Cabido (2001) hold for semi-arid and arid shrublands and woodlands, the most extensive rangelands in Australia.

The major findings of Díaz, Noy-Meir & Cabido (2001) that served as hypotheses for this study were that plant species that decrease in abundance under increased grazing pressure (decreasers) are characterized (in decreasing order of importance) by tall height, perennial life history, large (and thus, all else being equal, heavy) leaves and low specific leaf area (SLA), compared with neutral species and species that increase under increased grazing pressure (increasers). We need to know under what conditions these relationships between traits and grazing responses hold and, for situations where they do not hold, why this is. There are a number of possibilities for why these relationships may or may not hold in semi-arid and arid rangelands, which we outline below.

Height is hypothesized to decrease under increased grazing pressure because tall species receive most grazing pressure and short species are protected from grazing by tall species. This is based on the assumption that the groundstorey vegetation ($c. \leq 1$ m) is dense and that grazers take bites from above. However, in situations where grazers can take bites from the side and where short species are not protected by taller species, there may be no short species advantage. Such a situation may be encountered where vegetation is sparse, as in semi-arid and arid shrublands.

Leaf size is hypothesized to decrease under grazing pressure (Noy-Meir, Gutman & Kaplan 1989; Díaz, Noy-Meir & Cabido 2001) because larger leaves provide better bites for grazers, and smaller leaves require either more bites for a given leaf area (and mass) or include more stem material if taken in the same number of bites. This hypothesis should hold across all vegetation types.

Westoby (1999) suggested that SLA might be related to grazing responses in a different manner at low and high grazing intensity. At low grazing intensities, selective grazing on high SLA (thin, soft leaves) species may lead to their decreasing relative to low SLA species. However, under intense, non-selective grazing intensity, all species are grazed and high SLA species may be advantaged by faster regrowth, linked to faster leaf turnover and higher rate of return per gram of carbon invested in leaf tissue. Under conditions of set stocking in semi-arid and arid rangelands, grazing intensity and specificity may be affected by the amount of herbage available, which varies as a result of past rainfall (Westoby 1974; Landsberg *et al.* 2002). Thus the relationship between SLA and grazing response may be context-specific.

It is hypothesized that seed mass will decrease with grazing. This is because grazing removes above-ground biomass, creating open space. Grazers may also physically

disturb soil by feeding and walking. Both physical disturbance and open space create opportunities for colonization. Species able to take advantage of increased opportunities for recruitment are likely to be those that produce the greatest quantity of seed per unit biomass. As seed mass is inversely proportional to seed output per m^2 of canopy (Henery & Westoby 2001), smaller seeded species will have more colonization opportunities than large seeded species and so may increase in abundance under grazing (Westoby 1999). This hypothesis is likely to be true for vegetation types that are site-limited, such as dense vegetation. Semi-arid and arid shrublands have an open canopy and are not site-limited; instead recruitment occurs episodically in response to rainfall.

Annual species have been shown to increase at the expense of perennials under grazing pressure in many systems (Whalley, Robinson & Taylor 1978; Noy-Meir, Gutman & Kaplan 1989; McIntyre & Lavorel 2001). Under year-round grazing and relatively fixed growth seasons, annuals may allocate all resources to reproduction and avoid grazing consequences over unfavourable periods. In contrast, perennials maintain vegetative biomass and remain exposed to grazing during unfavourable periods (Bazzaz, Ackerly & Reekie 2000). Annuals also have greater reproductive allocation than perennials, which, all else being equal, means greater seed output (Bazzaz *et al.* 1987). Short generation times allow rapid exploitation of colonization opportunities due to grazing disturbance (Grime 1977). As for seed size (above), site limitation is not expected to operate in these open vegetation types. Also, growth seasons are fairly indeterminate for the majority of the sites studied here. Thus, annuals may not have strong advantages over perennials under grazing in these semi-arid and arid shrublands.

In this study we aimed to broaden empirical knowledge of how traits may be used to predict grazing responses under different conditions. We present tests of the above hypotheses on grazing responses for species of arid and semi-arid shrublands and woodlands of Australia. Previously published grazing studies were combined with trait data from previous surveys of plant traits (Leishman & Westoby 1992, 1994) and newly collected data to assess relationships between traits and grazing responses at several shrubland and woodland sites.

Methods and materials

DATA SETS

Lists of species' grazing responses from previously published grazing studies were collated in a previous study (Vesik & Westoby 2001). Briefly, species' responses to grazing were categorized as increaser (I), neutral (N) or decreaser (D) according to their change in abundance under increased grazing in published livestock grazing studies. A list of species and their responses

appears in Appendix S1 (see Supplementary material). The time periods of grazing treatment effects for most of the studies analysed here were *c.* 100 years (Appendix S2; see Supplementary material). Trait data for species were collated from a number of sources. Some traits came from a collation of species of western New South Wales, Australia, by M. R. Leishman (unpublished data), partially reported in Leishman & Westoby (1992, 1994). SLA data were added by M. R. Leishman (unpublished data). Other species data were collated by P.A. Vesk (unpublished data) from field collections and floras, especially Cunningham *et al.* (1992). Species nomenclature was updated according to the *Australian Plant Name Index* (Chapman 1991). Single publications could contribute multiple studies at different locations, e.g. Landsberg *et al.* (1997). Studies with less than 10 grazing responses for which we had trait data were excluded, yielding 15 studies. These were then further restricted to studies for which contrasts could be made between neutrals and decreaser or increaser species (Appendix S2).

PLANT TRAITS

Leaf size was optically scanned for at least two leaves from each of five individuals, and areas per leaf in mm² were calculated using Delta-T Scan (Kirchhof & Pendar 1993). After drying for at least 24 h at *c.* 65 °C, dry masses were measured and SLA calculated as area divided by dry mass (mm² mg⁻¹). Potential plant heights were generally maxima taken from the species' descriptions. Our aim was to capture the 'design height' reflecting strategic variation between species, not the realized height that may reflect responses to grazing, etc. (Westoby 1998). Where we had reliable observations from the field that conflicted, averages of the literature and field data were used. Growth form was classified as: woody shrub (1–4 m tall); woody subshrubs (< 1 m); forb (herbaceous, with or without woody base, including sedges, rushes and vines); grass. Species were classified as annual (1 year), short-lived (*c.* 2–5 years) or perennial (> *c.* 5 years), according to the literature. Seed mass was based on oven-dry seeds excluding dispersal structures (Leishman & Westoby 1994). A palatability score (1–5) was assigned to species based on rangeland handbooks (Vesk & Westoby 2001).

ANALYSES

The original intention was to perform identical analyses to those of Díaz, Noy-Meir & Cabido (2001), i.e. to compare the trait values of decreaser species with those of increaser and neutral species. However, it was not possible to carry out these analyses for three reasons: (i) species' grazing responses were obtained from several studies, and species often occurred in more than one study (to a differing degree between species); (ii) species' responses to grazing were not always consistent between different studies (Vesk & Westoby

2001); (iii) it transpired that aggregating neutral and increaser species obscured important patterns in the data. Hence, we first carried out broad analyses on a pooled data set and subsequently performed a meta-analysis of individual studies.

Pooled analyses

Species were pooled across studies into the three grazing responses (decreaser, neutral and increaser), then the trait values were substituted for species and compared for the response groups. We analysed both absolute and standardized trait values to see if the absolute value of the trait was less important than the value relative to the co-existing vegetation. As an example, if grazers were selecting the tallest species, then the relevant trait would be height relative to heights of the other species in the vegetation rather than height *per se*. However, results from the standardized trait values were consistent with those from the absolute data and so results from these analyses are not presented.

Leaf size, SLA, height and seed mass were all log₁₀-transformed prior to analyses, and prior to standardizing. ANOVA was used after checking that variances were homogeneous. Post-hoc comparisons of means used the Student–Newman–Keuls test (SNK; Sokal & Rohlf 1995).

For categorical traits (longevity, growth form and palatability) contingency tables were used and the likelihood ratio statistic was calculated (Agresti 1996). Adjusted residuals were used to indicate over- or under-representation in cells, for which absolute values greater than about 2 are noteworthy (Agresti 1996). Statistical analyses were performed using SPSS for Windows 10.0 (SPSS Inc., Chicago, IL).

Issues with pooling

Analysing the pooled data set had the virtues of simplicity and large sample size. However, species that occurred in more than one study would contribute more than one response, which could be considered as inflating the sample size. More importantly, species often had differing responses in different studies (Vesk & Westoby 2001). Hence a species and its trait value could potentially be represented in each of the decreaser, neutral and increaser groups. A species might have conflicting responses because species' trait values were advantageous or disadvantageous in differing situations, e.g. high vs. low mean annual rainfall, grazing intensity, grazing animal or density of co-existing species (Vesk & Westoby 2001). Ecotypic trait variation may also contribute to differing responses.

Meta-analysis

Because species could have conflicting responses in different studies, and to address concerns about pooling incompatible results, meta-analysis was used (Gurevitch, Curtis & Jones 2001). This allowed determination of

relationships between traits and the likelihood of one of two responses for each study in a consistent, comparable manner. In these analyses, each study was analysed separately to estimate size (and variance) of the effect that a particular trait had on the probability of a species being a decreaser, neutral or increaser. These effect sizes could then be combined to determine a mean effect, and confidence interval, over all studies analysed (Shadish & Haddock 1994). Responses were not binary, as most meta-analyses require, but could be decreaser, neutral or increaser. Initial exploration of the broad patterns in the data (as described in Pooled responses) indicated that differences between increaser and neutral species might be as great as between decrease and neutrals. Hence, two contrasts were used: decreaser vs. neutral and increaser vs. neutral.

Statistics describing effect size were then calculated. For categorical traits (annual, grass, etc.) 2×2 contingency tables were analysed to estimate the log-odds

$$\text{ratio, } \log_e \left[\frac{\left(\frac{p_1}{1-p_1} \right)}{\left(\frac{p_2}{1-p_2} \right)} \right], \text{ and its asymptotic standard error}$$

(ASE; Agresti 1996). This states how many times greater the odds, $p/(1-p)$, of being an increaser are for an annual compared with longer-lived species, for example. For quantitative traits, logistic regression was used to estimate the change in log-odds of being an increaser with a 10-fold increase in the trait, e.g. SLA, leaf size, potential height (Agresti 1996), using SPSS for Windows 10.0 (SPSS Inc.). All continuous traits were \log_{10} -transformed prior to analysis.

Random-effects meta-analysis models were used to estimate the grand mean effect size (and confidence interval) across studies (Raudenbush 1994). Meta-analysis was performed using Meta-Win 2.0 (Rosenberg, Adams & Gurevitch 1997). Routine checks for normality and heterogeneity among studies were made. Between-study variation was typically small, and in no case was it significant with Q -tests (Hedges 1994). In only one case was the pooled between-study variance more than 50% of the within-study variance, that being for the effect of being an annual on the odds of being a decreaser. All analyses met conditions of normality.

Results

WERE THERE BROAD ASSOCIATIONS BETWEEN TRAITS AND GRAZING RESPONSES?

Growth form

There was a significant association between grazing response and growth form [Table 1; likelihood ratio (LR) = 13.79, d.f. = 6, $P = 0.032$, $n = 441$ responses]. Shrubs were frequently neutral (adjusted residual = 3.4) and rarely increasers under grazing (adjusted residual = -2.0). In contrast, forbs tended to be increasers (adjusted residual = 1.7) rather than neutral (adjusted residual = -2.1).

Table 1. Grazing responses of species classified by growth form across all studies (expected numbers in parentheses). Data are numbers of responses; species can contribute more than one response and responses can be conflicting (in different studies)

Growth form	D	N	I	Total
Shrub	12 (15.3)	18 (9.5)	6 (11.3)	36
Subshrub	27 (25.4)	18 (15.8)	15 (18.8)	60
Forb	95 (93.3)	48 (57.9)	77 (68.8)	220
Grass	53 (53.0)	32 (32.9)	40 (39.1)	125
Total	187	116	138	441

Table 2. Grazing responses of species classified by life span across all studies (expected numbers in parentheses). Data are numbers of responses; species can contribute more than one response and responses can be conflicting (in different studies)

Life span	D	N	I	Total
Annual	53 (58.9)	22 (36.6)	64 (43.5)	139
Short lived	50 (42.4)	24 (26.3)	26 (31.3)	100
Perennial	84 (85.7)	70 (53.1)	48 (63.2)	202
Total	187	116	138	441

Table 3. Grazing responses of species classified by palatability, scored from 1 (high) to 5 (low) using species' descriptions (Vesk & Westoby 2001). Responses pooled across all studies (expected numbers in parentheses). Data are numbers of responses; species can contribute more than one response and responses can be conflicting (in different studies)

Palatability	D	N	I	Total
1	41 (35.4)	19 (23.0)	23 (24.6)	83
2	48 (46.9)	32 (30.5)	30 (32.6)	110
3	36 (41.4)	24 (26.9)	37 (28.7)	97
4	46 (46.1)	36 (30)	26 (32.0)	108
5	12 (13.2)	8 (8.6)	11 (9.2)	31
Total	183	119	127	429

Life span

There was a significant association between life span and grazing response (Table 2; LR = 27.16, d.f. = 4, $P < 0.001$, $n = 441$ responses). Perennial species were frequently neutral to grazing (adjusted residual = 3.7) and rarely increasers (adjusted residual = -3.1). In contrast, annuals were rarely neutral (adjusted residual = -3.4) and frequently increasers under grazing (adjusted residual = 4.5). Decreases by annuals were no fewer than expected by chance (adjusted residual = -1.2; Table 2).

Palatability

There was no association between the palatability score (Vesk & Westoby 2001) and grazing response at a broad level (Table 3; LR = 8.1, d.f. = 8, $P = 0.426$, $n = 429$ responses). This means that there was no evidence for highly palatable species being decrease, nor for unpalatable species being increasers.

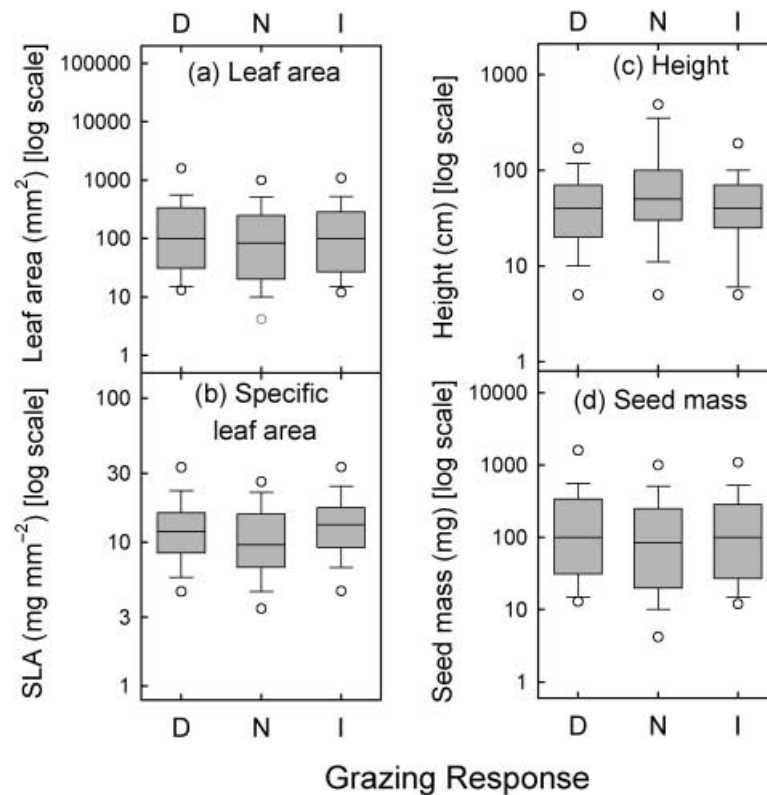


Fig. 1. Box plots of trait values for species' responses to grazing in Australian semi-arid shrub and woodlands. Responses have been pooled over all species and studies. D, decreaser; N, neutral; I, increaser. Height data are restricted to species below the shrub layer. Central line indicates median, box indicates 25th to 75th percentile, bars indicate 10th and 90th percentiles, circles are 5th and 95th percentiles.

Table 4. ANOVA summaries for quantitative trait differences between grazing response groups (D, N, I) across all studies. B, between groups; W, within groups. ** $P < 0.01$

Trait	Effect	d.f.	Mean square	F	P
Leaf size	B	2	0.838	1.90	0.151
	W	425	0.442		
SLA	B	2	0.293	5.33	0.005**
	W	416	0.055		
Height (< shrubs)	B	2	0.365	2.00	0.137
	W	437	0.182		
Seed mass	B	2	0.285	0.66	0.520
	W	390	0.434		

Continuous traits

At a broad level, SLA differed between grazing response groups but leaf size, height (subshrubs and lower) and seed mass did not (Fig. 1a–d and Table 4). Increasers had higher SLA than neutral species (Fig. 1b; SNK test, $P < 0.05$, $n = 109, 131$). Decreasers also tended to have marginally higher SLA than neutral species (Fig. 1b; SNK test $P = 0.053$, $n = 109, 179$). The tallest species (below the shrub layer) tended to show no response to grazing, although mean height was unrelated to grazing response (Fig. 1c). This effect was more pronounced when shrubs were included (data not shown), i.e. the taller subshrubs and shrubs were unaffected by the presence of grazers.

Medians for decreaser and increaser groups lay on the same side of the median for the neutral group for most traits, both when expressed as absolute values and relatively (Fig. 1). In other words, increasers and decreasers were not characterized by opposite ends of these spectra of variation.

Were there patterns within growth forms or life span classes?

There was no statistically significant effect of any term involving grazing response (as main effect, and two- or three-way interactions) using three-factor ANOVA (growth form, life span and grazing response as factors) for each of height, leaf size, SLA and seed mass ($P > 0.25$ in each case). Thus there was no evidence for effects operating within particular growth forms or life span classes. However, the observed power to detect main effects and interactions of grazing response was low [three-way: power = $(1 - \beta) = 0.17$ – 0.28 , two-way: power = $(1 - \beta) = 0.013$ – 0.050 , main effect: power = $(1 - \beta) = 0.07$ – 0.27]. This means that had there been a true effect or interaction, the chance of detecting it was less than 30% in all cases (Sokal & Rohlf 1995). To investigate further trends that might explain differences between these results and those of Díaz, Noy-Meir & Cabido (2001), separate one-way ANOVA for leaf size, SLA, height and seed mass were carried out within each growth form. No ANOVA was significant except for

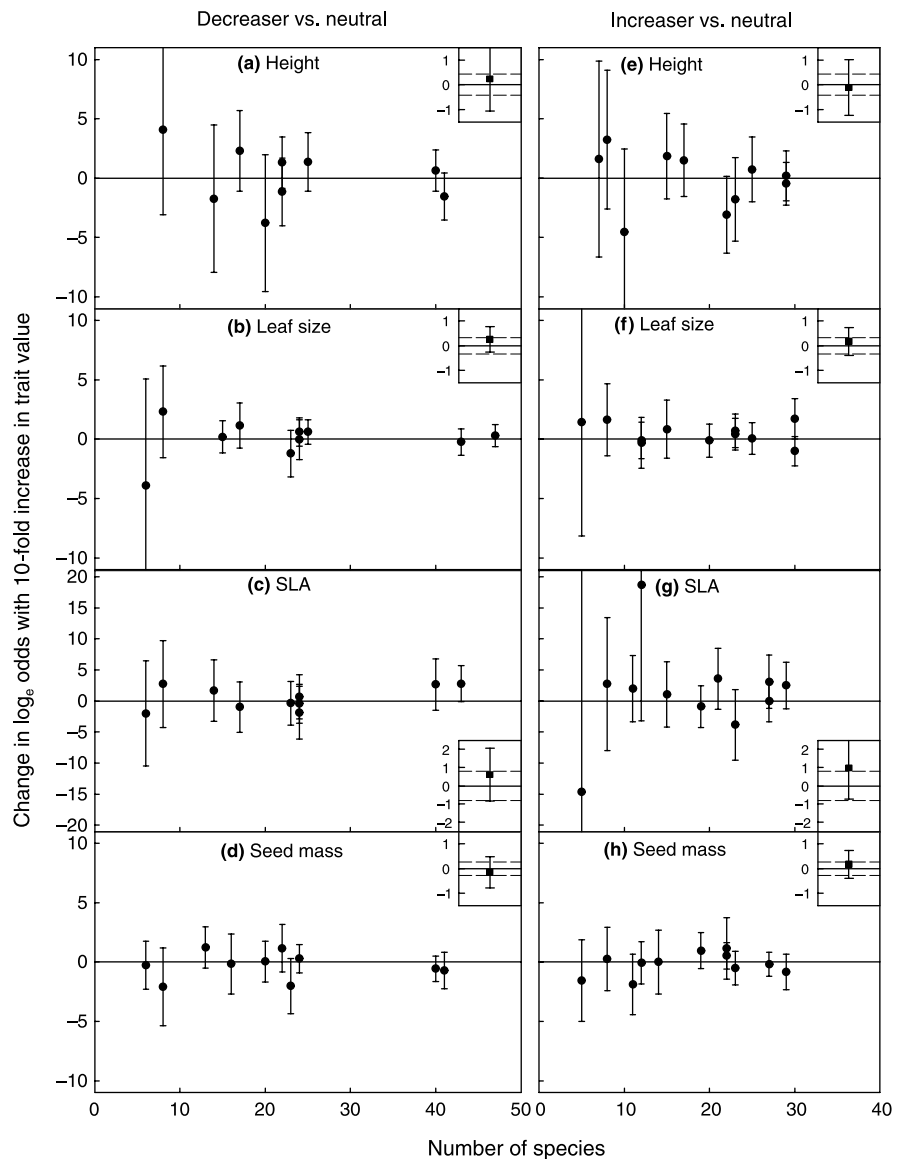


Fig. 2. Association between odds of being a grazing decreaser (a–d) or increaser (e–h) and the values of continuous species' traits. Each point represents one study. The x-axis is the number of species contrasted per study. The y-axis is the change in odds of being a decreaser (or an increaser) vs. neutral with a 10-fold increase in the trait value. Inserted graphs show the mean effect size and 95% confidence intervals, across studies. Dashed reference lines on the inserted graphs indicate where odds of showing a response are doubled for a shift from near lowest to near largest values (5th–95th percentile) of the trait.

SLA in grasses ($F_{2,120} = 5.18$, $P = 0.004$). Increaser grasses included 10 annual species (compared with one decreaser annual and no neutral annual grasses) and these had high SLA, lifting the mean SLA of increaser grasses.

WERE THERE RELATIONSHIPS BETWEEN TRAITS AND RESPONSES WITHIN STUDIES AND WERE THEY CONSISTENT ACROSS STUDIES?

The previous section examined broad patterns and failed to find strong relationships between species' traits and grazing responses. To check that this was not a result of pooling responses across studies, this section reports the meta-analysis results that analysed rela-

tionships within studies and then tested for combined effects across studies.

No striking relationships emerged between any measured traits and grazing response. Within studies, effects were nearly always weak enough for 95% confidence intervals to overlap zero (Figs 2 and 3). This means that within studies there were rarely significant effects of any trait on the odds of a particular grazing response. Neither was there an overall effect that was masked by small sample sizes within studies. For all continuous traits, the 95% confidence interval for mean effect size across all studies overlapped zero (Fig. 2, inserts). For example, on average the odds of being a decreaser nearly doubled with a 10-fold increase in leaf size, but this was not statistically significant (Fig. 2b, insert; dashed line indicates doubling of odds). Hence,

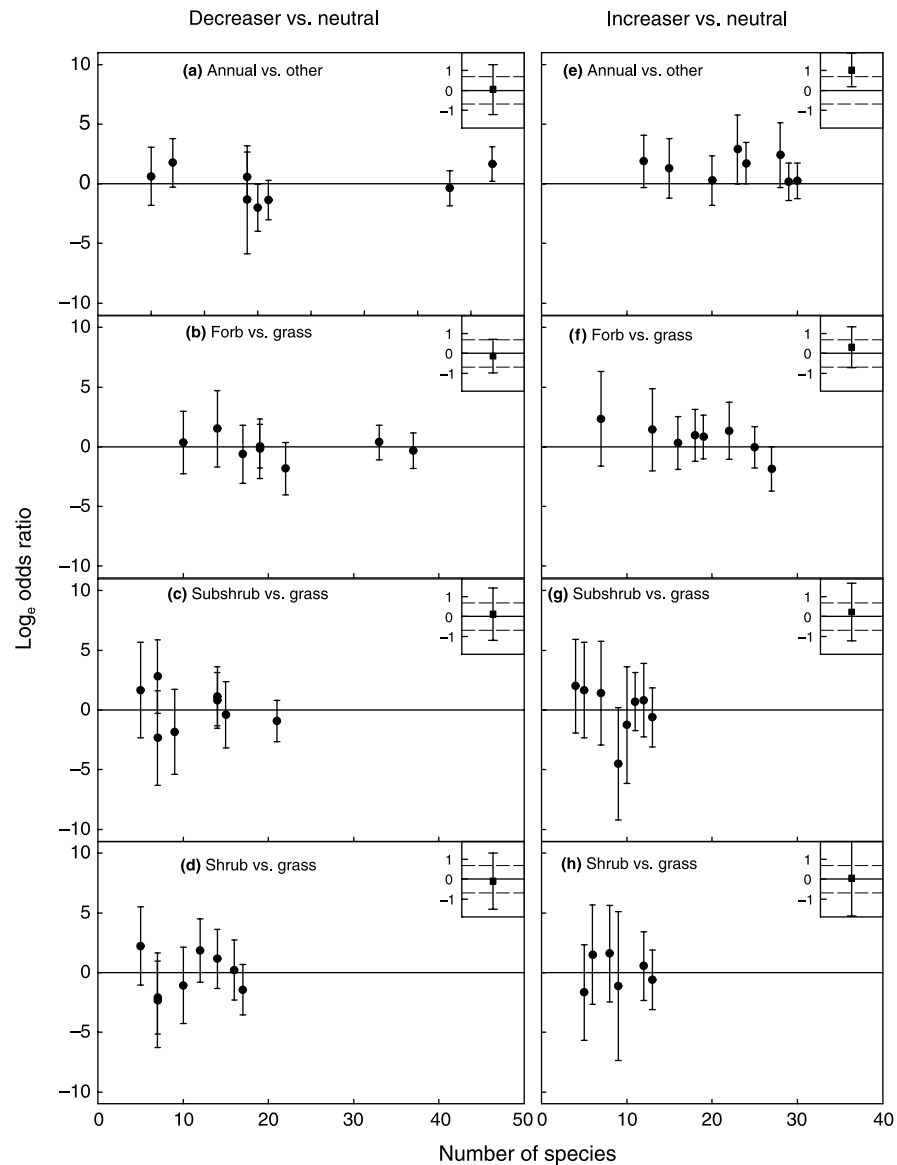


Fig. 3. Association between odds of being a decreaser (a–d) or increaser (e–h) and the values of categorical species' traits. Each point represents one study. The x-axis is the number of species contrasted per study. The y-axis is the log of the ratio of the odds of being a decreaser (a–d) or increaser (e–h) compared with neutral for the categories compared. Inserted graphs show the mean effect size and 95% confidence intervals, across all studies. Dashed reference lines on inserted graphs indicate where odds of showing a response are doubled for one class of the trait relative to the other, e.g. forb vs. grass.

we concluded that these traits did not have the capacity to predict grazing responses in the semi-arid shrublands and woodlands.

We then addressed specifically the patterns reported from grasslands in Israel and Argentina. In Australian shrublands and woodlands, taller species were not more likely to be decreasers (Fig. 2a) nor were short species more likely to be increasers (Fig. 2e). Larger leaved species were not more likely to be decreasers, nor were smaller leaved species more likely to be increasers. While a 10-fold increase in SLA more than doubled the odds of being an increaser, confidence intervals were wide and overlapped zero considerably (Fig. 2g, insert; dashed line indicates doubling of odds). For SLA (and to a smaller extent for leaf size), the size and direction

of the mean effect across studies was the same for both decreaser and increaser compared with neutral responses (Fig. 2).

Considering life span, across all studies the odds of annual species being increasers rather than neutral were, on average, 2.7 times better than longer-lived species (Fig. 3e, insert). There was no effect of growth form on likelihood of grazing response across studies (Fig. 3b–d, f–h).

Discussion

This study has shown that traits that have been shown to predict grazing responses in Argentine and Israeli subhumid grasslands (Díaz, Noy-Meir & Cabido 2001)

broadly failed to explain grazing responses in Australian semi-arid and arid shrublands and woodlands. There were no effects of plant height or leaf size on grazing responses. Annuals were more likely to be increasers in both the pooled analysis and meta-analysis. Forbs and high SLA species were more likely to increase in the pooled analyses, but not in the meta-analyses. The conservative interpretation would be to have greater confidence in the meta-analyses, as the pooled analyses had the characteristics of single species contributing multiple and often conflicting responses. Analyses of traits within growth forms (McIntyre *et al.* 1999) were limited in power but provided little evidence for relationships between traits and responses beyond annual grasses, which have high SLA leaves, being increasers.

We do not think that the difference in the analyses between the current study and that of Díaz, Noy-Meir & Cabido (2001) is the reason for discrepancies between the findings. While the details differed, if relationships with an explanatory power (r^2) ranging from 5% to 30% for single traits, were operating (as found by Díaz, Noy-Meir & Cabido 2001) the present analyses should have detected them. We believe that the important difference between the present study and the study by Díaz, Noy-Meir & Cabido (2001) is the vegetation structure. The Argentine and Israeli data were comprised solely of herbaceous species from productive grasslands bearing a continuous sward. Vegetation cover was > 90% for the Argentine sites (Díaz, Cabido & Casanoves 1998), and the Israeli sites achieved 100% cover each spring (Noy-Meir, Gutman & Kaplan 1989). Above-ground net primary production (ANPP) was *c.* 300 g dry matter (DM) m⁻² year⁻¹ at Argentine and Israeli sites (Díaz, Noy-Meir & Cabido 2001). In such a situation, grazers eat from top down and so, most importantly, tall species receive most grazing pressure and short species benefit by avoiding leaf loss and through relaxed competition (Díaz, Noy-Meir & Cabido 2001).

In contrast, in the Australian semi-arid and arid rangeland studies analysed here, more than 20% of responses were from shrubs and subshrubs, bare ground was frequent and ANPP was lower. Fine-tissue ANPP was estimated to be < 80 g DM m⁻² year⁻¹ for nine of the 11 sites in this study (Appendix S2; Barrett 2002). Bare ground and litter covered at least 50% of the ground in all eight grazing gradients studied by Landsberg *et al.* (1997) analysed here, and more than 90% in several gradients. As a result of these three factors (low productivity, growth form diversity and bare ground) grazers can move through vegetation and taller species do not necessarily receive greater grazing pressure. In addition, ground-layer species are more exposed to grazers as there are fewer tall species in the way. Hence, height is not so likely to be important as a trait, and simple traits in general are less likely to be good predictors of grazing response in semi-arid shrublands and woodlands (Landsberg, Lavorel & Stol 1999).

A previous detailed trait analysis of understorey species from two arid shrublands also studied here identified associations between increased grazing and small plant size, small leaves, high fecundity and plasticity of growth form (Landsberg, Lavorel & Stol 1999). However, Landsberg, Lavorel & Stol (1999) pointed out the overall lack of clear patterns and, as explanation, cited the complexity of grazing effects (selection, defoliation, altered recruitment opportunities) and lack of evolutionary history of ungulate grazing to provide selective pressure for clearly grazing-related traits (Landsberg, Lavorel & Stol 1999).

Unfortunately, we do not have data for comparable grassland sites to test whether the vegetation structure was the cause of the different results from Díaz, Noy-Meir & Cabido (2001). However, other work from subhumid Australian temperate grasslands (*c.* 780 mm, 400–600 g DM m⁻² year⁻¹ New South Wales northern tablelands; McIntyre, Lavorel & Tremont 1995) and subtropical open woodlands (*c.* 710 mm, ~300 g DM m⁻² year⁻¹ south-east Queensland; McIntyre & Lavorel 2001) has identified associations with increased grazing pressure for low height, small seeds and annual life history. This supports our idea that it is not the continent but the vegetation structure that is responsible for the differences between the results of this study and that of Díaz, Noy-Meir & Cabido (2001).

While we cannot discount possible explanations for the differing results being the dissimilar evolutionary history of grazing or that Australia is a 'special case', the most parsimonious explanation appears to be openness of vegetation due largely to low rainfall. Comparing different vegetation types are suggested as an avenue for further research.

DO INCREASERS AND DECREASERS HAVE OPPOSITE TRAITS, WITH NEUTRAL SPECIES INTERMEDIATE?

In most traits, increasers were more distinct from neutral species than decreasers. In several cases, decreasers were intermediate between neutral species and increasers. This was surprising, as Díaz, Noy-Meir & Cabido (2001) had pooled neutral and increaser species for their analyses, and the original intention here was to do the same. What is the cause of the apparent similarity in trait values of increasers and decreasers, and why were increasers more distinct as a group than decreasers?

One explanation is that there are many ways to be a decreaser, and fewer of being an increaser. For instance, long-lived palatable shrubs are targeted during dry periods when little other forage is available and thus they become decreasers near watering points, where grazers congregate. During good seasons, short-lived palatable species produce abundant nutritious foliage and are targeted when grazers are most selective in their diet and can forage farther from water (Landsberg *et al.* 2002). In contrast, increasers need to take advantage of open space and establishment opportunities

resulting from the activity of grazers. It is not enough to avoid or tolerate grazing. This would lead to a species being recorded as neutral. Species that reach most establishment sites, grow rapidly and reproduce early will tend to increase in abundance. In the shrublands and woodlands, annuals were more likely to be increasers (Noy-Meir, Gutman & Kaplan 1989; Belsky 1992).

Clearly, however, not all annuals were increasers. Annuals were unlikely to be neutral but no less likely than longer-lived species to decrease. Short generation times result in rapid increases (or decreases). Because of compounding effects over time, population-size shifts in short-lived species can become large and hence noticeable within a few years. In contrast, most long-lived species, especially shrubs, did not respond. As long as grazing does not hasten the death of mature plants, then decrease may not be detected by studies until individuals senesce without being replaced by recruiting juveniles (Andrew & Lange 1986). Thus on the time scales of these studies, persisting (or neutral) and increasing are different. For at least four of the studies for which we have data, grazing has had c. 100 years to exert effects on populations (Appendix S2).

Pooling traits of increasers and neutral species still seems intuitively reasonable. To increase in abundance, a species must maintain its population, i.e. not decrease. However, if species are actually decreasing over long time scales, but do not respond within the time frame and power of the study, then lumping increasers and neutrals will obscure relationships between traits and grazing responses. Increasers' traits may also differ from those of neutral species if they are invaders. Altered conditions for establishment and competitive interactions due to grazing provide opportunities for non-resident species to invade. Invaders do not need to be able to maintain a population at the site in the absence of grazing. As a result, invading species' traits may be distinct from neutral resident species.

These results should not diminish the enthusiasm for trait-based understanding of species' responses to grazing. A possible way forward is further analyses based on the same trait sets in situations that can be contrasted on a few fundamental axes, with annual rainfall and evolutionary history of grazing being primary ones (Milchunas & Lauenroth 1993).

Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JPE/JPE857/JPE857sm.htm>

Appendix S1 Species list with responses to grazing in various grazing studies in Australian shrublands and woodlands.

Appendix S2 List of grazing studies analysed, their locations and some environmental characteristics.

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