

Predicting plant species' responses to grazing

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Summary

1. The aim of this study was to identify whether plant species show consistent responses to livestock grazing. The analyses were based on 35 published studies from Australian rangelands providing 55 species response lists. The primary data set comprised 1554 responses from 829 species.

2. Eight-hundred and twenty-nine species were categorized as increasers, decreasers or neutral under grazing. Of 324 species that occurred in at least two response lists, 133 (41%) responded inconsistently, increasing at least once and decreasing at least once. While 59% of species responded consistently, these results suggest that our ability to predict vegetation change under grazing is limited.

3. Particular species were not inherently more or less consistent. Rather, as species occurred in more trials, the likelihood of at least one opposite response increased; no species that occurred at least eight times was wholly consistent. A binomial model indicated that the probability of an opposite response, across all species, was 0.275.

4. Contrary responses within species must result from context rather than from species' traits. Species were more likely to decrease in response to grazing at lower rainfall than at higher rainfall. Forbs tended to increase under grazing at sites where wet seasons were cooler. Changing the grazing animal was weakly correlated with change in response direction, although not enough for it to be useful for manipulating pasture composition. We found little support for ideas that different responses within species are due to differences in alternative forage available, or due to non-linearity of response to grazing intensity.

5. At present it appears we can predict species response direction about three-quarters of the time, at a continental scale. This represents an upper limit of the reliability of prediction based on species' traits alone. Presently we do not know what aspects of the context might allow us to predict reliably the remaining one-quarter of responses.

Key-words: Australia, consistency, ecological synthesis, increaser, range condition, vegetation change.

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Introduction

Changes in plant species composition are central to range management for sustainable production and off-reserve conservation (Stoddart, Smith & Box 1975; Curry & Hacker 1990; James, Landsberg & Morton 1995; Morton *et al.* 1995). Plant species can be characterized as increasers or decreasers corresponding to their shifts in relative abundance in response to grazing. There is a long tradition of assessing the position of rangelands along a condition spectrum by characterizing the relative abundance of increaser and decreaser species previously identified from grazing surveys and trials (Sampson 1917; Dyksterhuis 1949). Later ideas about

rangelands do not assume a single linear condition spectrum, nor that shifts along the spectrum necessarily occur smoothly in response to grazing pressure, but are still based around plant species' responses to grazing (Westoby 1980; Walker *et al.* 1981; Griffin & Friedel 1985; Westoby, Walker & Noy-Meir 1989).

Many studies have investigated the effects of grazing on plant species composition, and much knowledge exists on species' responses in particular rangeland situations, with the implicit expectation that the results may be extrapolated to other situations. These studies include formal stocking rate trials (Williams 1969; McIvor 1998), exclosures (Grice & Barchia 1995; Meissner & Facelli 1999) and a variety of gradient analyses utilizing land-use records (Biddiscombe 1953; Tiver & Andrew 1997; Fensham 1998), distance from watering points (Andrew & Lange 1986; Landsberg

et al. 1997b) and range condition indices (Friedel 1981; Hacker 1987; McIvor, Ash & Cook 1995).

The work here compiled Australian studies with a view to two initial aims: (i) to synthesize field-based knowledge of species' responses to grazing; (ii) to serve as a background for planned work to identify plant traits characterizing increasers and decreasers. There is presently an ongoing international effort to identify plant functional types and traits related to disturbance response for the purposes of predicting vegetation dynamics (Lavorel *et al.* 1997; McIntyre *et al.* 1999 and other papers in that issue of the *Journal of Vegetation Science*; Sternberg *et al.* 2000; Bullock *et al.* 2001; Watkinson & Ormerod, 2001). This effort requires knowledge of what species do in common and what are the main spectra of among-species variation.

In compiling the data for this synthesis, substantial inconsistency in species' responses emerged. If a species responds in different ways in different trials, the response can not be predicted reliably from the traits of the species alone. Consequently this paper overviews Australian grazing studies and quantifies the levels of consistency and inconsistency in species' responses. In the terminology of Gitay & Noble (1997), we assessed the repeatability of the increaser and decreaser response groups. This is important for specifying the domain over which species' traits may be useful for understanding and predicting responses. Where responses are inconsistent, then other aspects of the situation, such as other species present and their relative palatability, the species of grazing animal or rainfall at the site, might potentially explain the different outcomes. We investigated such case-specific variables to the extent possible with the data available.

Methods

DATABASE

The following electronic databases were searched: Current Contents (1998–99), Biological Abstracts (1991–97), Agricola (Agricultural Online Access; 1979–99), CAB (Commonwealth Agricultural Bureau; 1973–99), ABOA (Australian Bibliography of Agriculture; 1975–99), ARRIP (Australian Rural Research in Progress; 1984–99) and CARRP (Completed Australian Rural Research Projects; 1984–99). Entire publication histories of the *Rangeland Journal* (formerly *Australian Rangeland Journal*) and *Australian Journal of Ecology* were searched (both 1976 to present). We traced further studies from reference lists of papers. To be included studies had to: (i) be published in peer-reviewed open journal publications; (ii) be carried out in unimproved pasture, overstorey clearing was permitted but not sowing (with one exception indicated below), fertilization or irrigation; (iii) report change in species composition, providing primary data even if only as presence/absence or as graphs. Literature surveys and purely verbal descriptions were not included. We believe the

resulting list (Table 1) is a comprehensive sample of studies in Australia meeting these criteria. A recent study of several grazing gradients was included despite only an outline of results being published in an open journal (Landsberg, James & Morton 1997a) because detailed results were available in a report (Landsberg *et al.* 1997b). We included one study of reseeded degraded rangeland because the understorey dominants resembled those in the original situation (Hacker & Tunbridge 1991).

Thirty-five studies presented data on species composition changes (Table 1). These studies yielded 55 species response lists, covering a wide spread of both geographical locations (latitude 15°–38°S, longitude 114°–153°E; Fig. 1) and range types. There were eight semi-arid woodlands, seven subtropical and tropical woodlands, eight temperate grasslands and grassy woodlands, 10 arid and dry tropical grasslands (*Astrelba* and *Dichanthium*), 13 chenopod shrublands, seven *Acacia* shrublands, one alpine grassland and one arid open woodland. Grazing response lists (number in parentheses) used fenceline contrasts (one), stocking rate trials (nine, including one high-intensity rotational trial), exclosures (nine), mowing (one) and several types of gradient analyses (34). Grazing gradients were identified using land-use records (10), distance to watering points (13), transects across paddocks to sheep camps (two) and various range condition indices (nine).

Data relating to each study were entered into the database. In some cases latitudes, longitudes and elevations had to be estimated using site descriptions and by consulting maps. Where grazing response sites corresponded to weather stations, data from the weather station were used for estimating mean annual rainfall. Otherwise the Australian climate-interpolating software BIOCLIM was used to characterize the climate under which the vegetation had developed (Nix 1986; Hutchinson *et al.* 1997). BIOCLIM interpolates from neighbouring stations using elevation and latitude and longitude of sites. As a test of the reliability of these estimates, the rainfall of sites was regressed against the rainfall predicted by BIOCLIM, yielding good agreement ($r^2 = 0.99$, $n = 56$).

Plant species from studies were classified as decreasers, neutral or increasers (D, N, I, respectively) under grazing. Some studies distinguished monotonic from non-linear unimodal responses to grazing intensity (e.g. Hacker 1987; Fensham, Holman & Cox 1999). Certain studies also allowed the relative intensity at which abundance was maximal (the peak) to be determined. However, information for this fine-scale classification was lacking for the majority of cases. Hence, most analyses were carried out at the level of D, N or I. Responses were determined in papers in a number of ways: significance test of a contrast among levels of a grazing experiment; presence on only one side of a contrast between grazed and exclosed plots; fenceline contrasts; significant relation to a putative grazing gradient, for example distance from a watering point or distribution along a gradient on an ordination of

Table 1. Grazing response lists and general characteristics of the studies. Grazer: the animal whose density was changed as part of the study design, kangaroo grazing is likely to be a significant pressure in most studies, S = sheep, C = cattle, K = kangaroo. Study type: G = gradient analysis, W = distance to water, L = land use, E = enclosure experiment, R = range condition, F = fenceline contrast, S = stocking rate trial, T = tactical stocking, H = high-intensity rotational stocking trial, C = sheep camp, M = mowing. Response determination is the method used to determine the species' responses for the purposes of the current study: I = intensity, Tm = time, Tr = trend, Ts = significance test, 2× = doubling, P = presence/absence, R = regression, A = association including correspondence analysis, C = contrast

List	Reference	Vegetation	Grazer	Study type	Response determination	Longitude (°)	Latitude (°)	Altitude (m a.s.l.)	Rain (mm year ⁻¹)
1	Andrew & Lange (1986)	Chenopod shrubland	S	G, W	I Ts R	137.38	-32.88	40	223
2	Barker & Lange (1969)	Chenopod shrubland	S	G, W	I Ts R	140.2	-33.2	120	236
3	Biddiscombe (1953)	Semi-arid grassy woodland	S	G, L	I Tr	147.98	-32.03	219	465
4	Biddiscombe (1953)	Semi-arid grassy woodland	S	G, L	I Tr	147.98	-32.03	219	465
5	Foran & Bastin (1984)	Arid (<i>Astrelba</i>) grassland	C	E	I Ts C	133.92	-18.2	260	407
6	Foran & Bastin (1984)	Arid (<i>Astrelba</i>) grassland	C	G, W	I Tr	133.92	-18.2	260	407
7	Fensham (1998)	Dry tropical (<i>Dichanthium</i>) grassland	S, C	G, L	I Ts A	151.5	-27.25	500	653
8	Fensham (1998)	Subtropical grassy woodland	S, C	G, L	I Ts A	151.5	-27.25	500	647
9	Fensham (1998)	Subtropical grassy woodland	S, C	G, L	I Ts A	151.5	-27.25	550	689
10	Fensham, Holman & Cox (1999)	Dry tropical (<i>Dichanthium</i>) grassland	S, C	G, L	I Tr	148.25	-23.25	300	701
11	Friedel (1981)	Arid (<i>Astrelba</i>) grassland	C	G, R	I Tr	133.84	-23.7	580	263
12	Friedel (1981)	Arid open woodland	C	G, R	I Tr	133.84	-23.7	580	263
13	Friedel (1981)	Acacia shrubland	C	G, R	I Tr	133.84	-23.7	580	263
14	Friedel (1997)	Chenopod shrubland/arid grassland	C	G, W	I Tr A	134	-25	500	200
15	Grice & Barchia (1995)	Semi-arid grassy woodland	S, K	E	I Ts C	144.8	-31.5	250	300
16	Grice & Barchia (1995)	Semi-arid grassy woodland	S, K	E	I Ts C	144.8	-31.5	250	300
17	Grice & Barchia (1995)	Semi-arid grassy woodland	S, K	E	I Ts C	144.8	-31.5	250	300
18	Graetz (1986)	Chenopod shrubland	S	F	I Ts C	141.05	-30.83	140	185
19	Hacker (1983)	Acacia shrubland	S	G, R	I Tr A	121.7	-29.1	350	198
20	Hacker (1984)	Acacia shrubland	S	G, R	I Tr A	121.7	-29.1	350	198
21	Hacker (1987)	Chenopod shrubland	S	G, R	I Tr A	121.7	-29.1	320	198
22	Hall & Lee (1980)	Arid (<i>Astrelba</i>) grassland	C, S	S	Tm Tr	141.8	-21.03	149	444
23	Hall & Lee (1980)	Arid (<i>Astrelba</i>) grassland	C, S	S	I P C	141.8	-21.03	149	444
24	Hacker & Tunbridge (1991)	Tropical grassy woodland	C	E, T	I Ts C	128.92	-17.39	170	579
25	Landsberg <i>et al.</i> (1997b)	Acacia shrubland	C	G, W	I Tr A/R	132.7	-25.7	500	196
26	Landsberg <i>et al.</i> (1997b)	Acacia shrubland	S, C	G, W	I Tr A/R	144.5	-29.3	120	290
27	Landsberg <i>et al.</i> (1997b)	Acacia shrubland	S	G, W	I Tr A/R	143.4	-24.8	150	285
28	Landsberg <i>et al.</i> (1997b)	Acacia shrubland	S	G, W	I Tr A/R	144	-26.8	190	308
29	Landsberg <i>et al.</i> (1997b)	Chenopod shrubland	S	G, W	I Tr A/R	114.2	-24.3	40	203
30	Landsberg <i>et al.</i> (1997b)	Chenopod shrubland/ <i>Acacia</i> shrubland	S	G, W	I Tr A/R	136.3	-31.6	160	185
31	Landsberg <i>et al.</i> (1997b)	Chenopod shrubland	S	G, W	I Tr A/R	137.5	-31.7	100	182

Table 1. (cont'd)

List	Reference	Vegetation	Grazer	Study type	Response determination	Longitude (°)	Latitude (°)	Altitude (m a.s.l.)	Rain (mm year ⁻¹)
32	Landsberg <i>et al.</i> (1997b)	Chenopod shrubland	S	G, W	I Tr A/R	126.9	–31.5	100	280
33	Lodge & Whalley (1985)	Grassy woodland/temperate grassland	S	H	Tm Tr	150.7	–31	400	670
34	McIvor, Ash & Cook (1995)	Dry tropical (<i>Dichanthium</i>) grassland	C	G, R	I Tr A	131.4	–15.5	200	780
35	McIvor, Ash & Cook (1995)	Tropical grassy woodland	C	G, R	I Tr A	131.94	–14.8	120	900
36	McIvor (1998)	Tropical grassy woodland	C	S	I Tr A	146.7	–20.2	240	670
37	McIvor (1998)	Tropical grassy woodlands	C	S	I Tr A	145.79	–19.7	300	546
38	McIntyre & Lavorel (1994)	Grassy woodland/temperate grassland	S	G, R	I Tr A	151.75	–30.25	1000	780
39	Meissner & Facelli (1999)	Chenopod shrubland	S	E	I Ts C	137.4	–32.95	40	215
40	Ogders & Rogers (1993)	Subtropical grassy woodland	Mower	L, M	I P C	152.95	–27.48	227	1274
41	Orr (1980a,b)	Arid (<i>Astrebla</i>) grassland	S	G, L	I Tr	145.45	–24.42	280	520
42	Orr (1981)	Arid (<i>Astrebla</i>) grassland	C	E	Tm Tr, I C	146.2	–28.1	190	375
43	Prober & Thiele (1995)	Grassy woodland/temperate grassland	S, C	G, L	I Tr A	149.0	–33.5	400	650
44	Rogers & Stride (1997)	Semi-arid grassy woodland	S, few C	G, W	I Ts R	146.03	–28.15	190	371
45	Rogers & Whalley (1989)	Grassy woodland/temperate grassland	S	G, C	I Tr	151.4	–30.3	1100	800
46	Robards, Michalk & Pither (1978)	Semi-arid grassy woodland	S	S	Tm Tr, I C	147.95	–31.99	215	497
47	Robards, Michalk & Pither (1978)	Semi-arid grassy woodland	S	S	Tm Tr, I C	147.95	–31.99	215	497
48	Stuwe & Parsons (1977)	Temperate grassland	S, C	G, L	I Ts A	144.2	–37.5	200	562
49	Tiver & Andrew (1997)	Chenopod shrubland	S	G, L	I Ts R	140	–32.5	250	237
50	Trémont (1994)	Grassy woodland/temperate grassland	S	S	I 2× C	151.53	–30.62	1060	800
51	Wahren, Papst & Williams (1994)	Alpine grassland	C	E	Tm Tr, I C	147.2	–36.54	1700	2317
52	Whalley, Robinson & Taylor (1978)	Grassy woodland/temperate grassland	S	G, C	I Tr	151.69	–29.7	1060	850
53	Whalley, Robinson & Taylor (1978)	Grassy woodland/temperate grassland	S	S	Tm Tr	151.69	–29.7	1060	850
54	Williams (1969)	Chenopod shrubland/semi-arid grassland	S	S	Tm Tr, I C	144.9	–35.5	93	415
55	Yan, Holm & Mitchell (1996)	Chenopod shrubland	S	E, T	Tm Tr, I C	115.5	–27.25	450	218

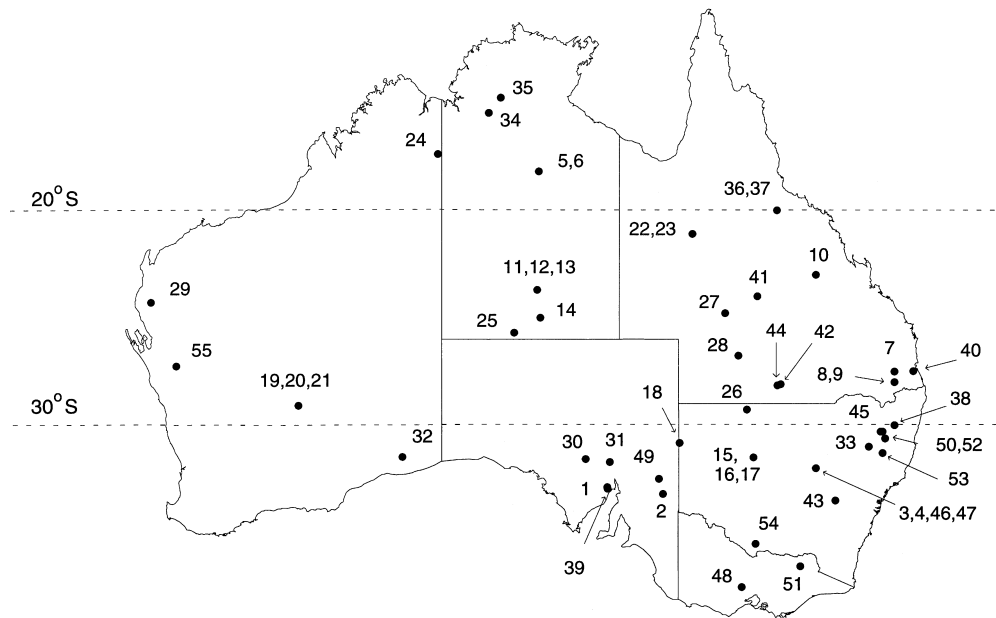


Fig. 1. Distribution of mainland Australian grazing studies from the literature reporting species composition changes in vegetation. Numbers refer to grazing response lists in Table 1.

community composition. Some responses were classified by species' abundances being doubled in one level relative to the other in the contrast of grazed and enclosed plots; this was used where abundances were low, i.e. statistical power was low (e.g. Trémont 1994). We determined responses for several studies subjectively from trends through time or across grazing intensities (e.g. Biddiscombe 1953; Friedel 1981; Fensham, Holman & Cox 1999). While this subjectivity was undesirable, the great majority of rangeland grazing studies are not fully replicated, long-running, powerful experiments allowing clear significance tests of responses. To use the wealth of information available effectively, optimal meta-analyses utilizing effect size were not possible (Osenberg *et al.* 1999). The meta-analysis technique closest to the method used here is vote-counting (Hedges & Olkin 1980).

Sometimes a single publication contributed more than one list of responses (Table 1). One publication in particular (Landsberg *et al.* 1997b) contributed a considerable number of species response lists. We investigated whether overall patterns were unduly influenced by the response lists from this particular study. Nomenclature followed Harden (1990), George (1982) or Black (1965).

Results

CONSISTENCY OR OTHERWISE?

The primary data set comprised 1554 responses from 829 species. There were an additional 183 responses from 55 species defined as overstorey (> 0.5 m high) by Landsberg *et al.* (1997b). These were not examined in the majority of the analyses presented here. Of the 829 species in the primary data set, 505 species occurred

only once. Three-hundred and twenty-four species occurred at least twice; these appear in Appendix 1 (see Supplementary material, p. 918).

One-hundred and thirty-three of the 324 species (41%) that occurred at least twice were classified D at least once and I at least once, and are referred to as inconsistent (ID) (Table 2). The proportions of species in the different response classes (consistent I, N, D and ID) were generally consistent across the data from understorey and overstorey in the studies of Landsberg *et al.* (1997b) and from the remainder of the studies (Table 2).

Considering all species that occurred more than once, the incidence of at least one conflicting response (ID species) increased as species occurred in more response lists (Fig. 2, filled circles). All 14 species that occurred at least eight times exhibited at least one conflicting response. This suggests the situation is best thought of not so much in terms of distinguishing species that show consistent vs. inconsistent responses, but more in terms of some probability of obtaining a conflicting response, applying across species and cases.

As an index of inconsistency for each species, the minority of the two results (D or I) was expressed as a proportion of the number of responses. Only D and I responses were used; N were omitted and the number of responses adjusted. The distinctions between N and I or D were blurred by differences among studies in the way that responses were attributed. Also, we considered that a binary approach, i.e. I or D, was simpler. Where I = D either was used as the minority. The maximum of this index was 0.5. This index was averaged over each set of species with equal number of occurrences. The mean proportion of minority responses over all cases was $P = 0.21$ (proportion of minority responses summed over all species divided by the total

Table 2. Abundance responses of plant species that occur in multiple grazing response lists from Australian studies. Species were categorized as consistent increasers, decreasees or neutral, or as responding inconsistently in different lists. Terms in parentheses show percentages and further break down of categories into species that showed: only increases (II), increases and neutral responses (IN), only decreasees (DD), decreasees and neutral responses (DN), increases and decreasees (ID) and, increases, decreasees and neutral responses (IND). Columns represent breakdown of the primary data set to examine the impact of one study (Landsberg *et al.* 1997b) contributing a large proportion of the data. The columns are not exclusive. Overstorey species from Landsberg *et al.* (1997b) were not used in the primary data set

	Primary data set	Omitting Landsberg <i>et al.</i> (1997b) data	Landsberg <i>et al.</i> (1997b) understorey data	Overstorey: Landsberg <i>et al.</i> (1997b) and others
Consistently increased	77 (23%; 46 II, 31 IN)	66 (34%; 42 II, 24 IN)	15 (11%; 4 II, 11 IN)	18 (21%; 11 II, 7 IN)
Consistently decreased	96 (30%; 42 DD, 54 DN)	50 (26%; 26 DD, 24 DN)	56 (43%; 22 DD, 34 DN)	29 (34%; 4 DD, 25 DN)
Consistently neutral	18 (6%)	5 (3%)	13 (10%)	14 (16%)
Inconsistently responded	133 (41%; 61 IND, 72 ID)	72 (37%; 18 IND, 54 ID)	47 (36%; 25 IND, 22 ID)	25 (29%; 20 IND, 5 ID)
Total number of species with multiple occurrences	324	193	131	86

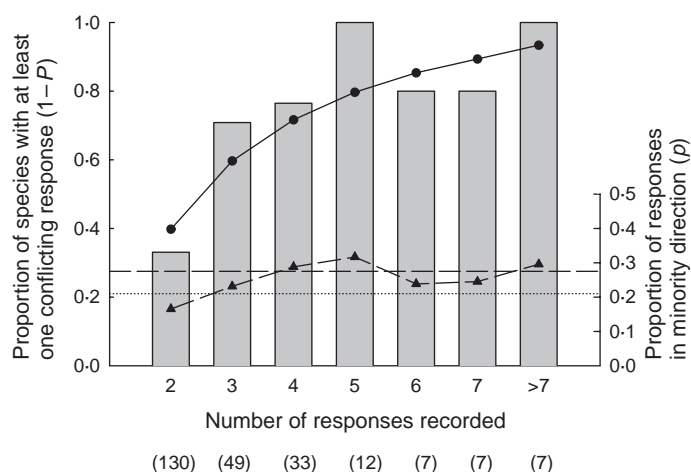


Fig. 2. Consistency of grazing response direction (increase or decrease) in Australian rangeland plants and the effect of multiple trials. The observed proportions of species ($1 - P$) with at least one conflicting response increased with the number of trials in which a species occurred (columns). The dotted line is the grand mean proportion of minority responses by species across all responses. The mean proportion of minority responses by species (p , triangles) initially increased with number of responses recorded for a species. A binomial model, $P = p^n + (1 - p)^n$ (filled circles), fit to the observed proportions of species with at least one conflicting response, indicated that the true minority response probability was $p = 0.275$ (long dashed line). The number of species in each class appears below the columns.

number of responses). However, this probably underestimates the true probability of a minority response. Particularly for species with only two responses recorded, there must be some chance that all recorded responses are in a direction that would have been the minority if a large number of responses had been recorded. In line with this, the proportion of minority responses recorded was lower when few responses had been recorded (Fig. 2, triangles). To adjust for this effect, we used the binomial formula:

$$P = p^n + (1 - p)^n \quad \text{eqn 1}$$

If p is the true probability of a minority response given a large number of observed responses, then P is the probability that a species will show consistent responses, depending on the number of responses observed n , and including the chance of getting all ‘minority’ responses p^n as well as the chance of getting all majority responses $(1 - p)^n$. The value of p that

minimized the difference between the observed and expected numbers of consistent responses when summed across all numbers of responses ($n = 2, 3, \dots$), and using the observed numbers of species for each number of responses, was $p = 0.275$. We again used the binomial formula to calculate the expected proportion of inconsistent species ($1 - P$) for each number of responses for $p = 0.275$ (Fig. 2, columns). This showed an increase with number of occurrences, saturating in a similar fashion to the observed result, allowing for sampling variation.

We do not argue that this estimate of 1-in-4 responses being in a minority direction applies completely uniformly across all species. It would be surprising if there were not differences between species in how consistently they behaved. Two species showed zero minority out of seven responses (*Dichanthium sericeum* D = 6, N = 1; *Urochloa panicoides* I = 7). Minority response proportions for ID species ranged from 0.083 (I = 1 and D = 11) for *Themeda triandra* and 0.11 for *Chloris*

truncata (I = 8 and D = 1) to the maximum of 0.5 for a number of species, notably *Aristida contorta* (I = 4, D = 4) and *Tripogon loliiformis* (I = 4, D = 4) (Appendix 1). On the other hand, none of the species represented by eight or more responses behaved wholly consistently. It would clearly be a mistake to suppose that all the species represented by two consistent responses would remain consistent given a larger number of responses.

POTENTIAL EXPLANATIONS FOR INCONSISTENCY

A 1-in-4 incidence of minority responses appeared substantial, considering the strong tradition in the literature suggesting it should be possible to label species as either I or D under grazing. Consequently, we investigated some possible explanations for inconsistencies. Logically, inconsistencies might arise either from differences in species' traits between sites, or from differences in the abiotic or biotic context between sites. Lacking details of ecotypic variation between study sites for each species, we were unable to test formally for that possibility. However, we do not believe it is credible that a 1-in-4 incidence of reversals of grazing response results from within-species variation in traits. This would represent misallocation of species boundaries on a startling scale. Further, species known to include much ecotypic variation, such as *Themeda triandra* (Cunningham *et al.* 1992), showed relatively little inconsistency of response.

It seems far more likely that inconsistencies arise from differences between sites with regard to climate, soils, grazing animal or vegetation. The possibilities we were able to investigate were rainfall amount and seasonality, availability of alternative palatable forage, shape of response to grazing intensity, and the grazing animal. These were all investigated at the species level. Data for the explanatory variables were compared pairwise using the mean value of the variable in question for I cases compared with the mean value for D cases. The quality of data made it difficult to draw clear inferences from the last three possibilities in particular. These somewhat inconclusive tests are outlined briefly to save other workers from retracing our tracks.

Mean annual rainfall

Aridity and grazing may combine in their effect on plants (O'Connor 1991; Hodgkinson & Cook 1994). Defoliation by grazers may reduce a plant's ability to cope with drought, while water limitation may reduce a plant's capacity to recover from defoliation (Coughenour, McNaughton & Wallace 1985; Busso & Richards 1995). Consequently, we compared the mean annual rainfall at sites where ID species increased with sites where they decreased. Although soil type clearly affects site productivity, scant data were available. An analysis of the relationship of broad soil types to response consistency was inconclusive.

For species that responded inconsistently to grazing, it did indeed prove significantly more likely that they increased at higher rainfall locations and decreased at lower rainfall locations than the reverse [pairwise difference $t = 2.89$, d.f. = 132, $P = 0.005$, mean difference 47 ± 32 mm year⁻¹, 95% confidence interval (CI)].

The proportion of species that responded in the minority direction at a site was not correlated with rainfall or any other site variable.

Seasonal distribution of rainfall

Some species might have been D at sites where the season when most rain falls was suboptimal for their phenology. Species are often characterized by the season in which they grow fastest, for example many grasses, particularly species with C₄ metabolism, respond best to warm season rainfall (Harrington *et al.* 1984). To assess seasonal distribution of rainfall, we used the mean temperature of the wettest quarter of the year. This was correlated with the coefficient of variation (CV) of mean monthly rainfalls ($r = 0.56$, $n = 55$, $P < 0.01$) but uncorrelated with annual rainfall ($r = -0.02$, $n = 55$, $P = 0.90$). Similarly, annual rainfall differences between sites where a species increased or decreased were uncorrelated with differences in the mean temperature of the wettest quarter ($r = 0.10$, $n = 133$, $P = 0.25$). Hence, the patterns that follow are not side-effects of total rainfall.

Species that responded inconsistently to grazing tended to increase at sites where the temperature of the wet season was cooler than where they decreased ($t = -2.57$, d.f. = 132, $P = 0.011$). Analysing life-form groups separately, forb species definitely tended to be grazing I where wet seasons were cooler ($t = -2.76$, d.f. = 70, $P = 0.007$, mean difference of $-2.31 \pm 1.67^\circ$, 95% CI). Grazing responses of graminoids were unrelated to wet season temperature ($t = 0.31$, d.f. = 51, $P = 0.76$), differing from forbs ($F_{(1,121)} = 4.90$, $P = 0.029$). There was no clear pattern of rainfall seasonality effects on response direction for grasses in relation to carbon pathway (C₃ vs. C₄). This may have been because within C₄ grasses the different biochemical subtypes (NAD, NADP, PCK; see Hattersley 1992) had different responses to wet season temperature (data not shown), but patterns at this level had sample sizes too small to be convincing. Hattersley (1992) showed that NAD and NADP subtypes differ in their geographical distribution in relation to rainfall and that more NAD species are found at higher summer temperatures. Trees and shrubs (understorey and overstorey) tended weakly to increase under grazing at sites where wet seasons were cooler ($t = -1.78$, d.f. = 15, $P = 0.095$, mean difference $-3.50 \pm 4.19^\circ$).

Rainfall in Australia is summer-dominant in the north (monsoon related) and winter-dominant in the far south, with intermediate and uniform (although variable) year-round rainfall in between (Fitzpatrick & Nix 1973). Hence latitudinal differences among sites

were examined to see whether the difference in seasonality that we detected using the mean temperature of the wet quarter might be interpretable as a latitudinal effect. For the sites where multiple occurring species were recorded [excluding Wahren, Papst & Williams (1994), which was the only alpine site], latitude was highly correlated with rainfall seasonality, as measured by the CV of monthly rainfall ($r = 0.95$, $n = 55$, $P < 0.001$), such that variation between months increased towards the tropics. Latitude was also correlated with mean temperature of the wettest quarter ($r = 0.68$, $n = 55$, $P < 0.001$). However, there was no significant difference between latitudes of sites where species were recorded as grazing I and D ($t = 0.05$, d.f. = 132, $P = 0.96$); similarly when grasses and forbs were treated separately (forbs: $t = -0.48$, d.f. = 70, $P = 0.63$; graminoids: $t = 1.11$, d.f. = 51, $P = 0.27$). This result may be explained by opposite tendencies of I responses with higher rainfall and lower wet season temperature. While the relationship between rainfall and latitude is weak, it is enough to prevent latitude explaining inconsistency.

Relative palatability and diet selection

One obvious possibility is that grazers may have been eating different plant species in different situations. Large generalist herbivores such as sheep and cattle select a range of the most palatable foods from the available forage (Westoby 1974; Stoddart, Smith & Box 1975; Owen-Smith & Novellie 1982; Wilson & Harrington 1984). Whether or not a species is eaten depends upon what else is available. Hence a species' palatability is relative, not absolute. Grazer impact on a species is thus expected to be high when it is clearly the most palatable available, and lower when other species of similar or greater palatability contribute substantial cover or biomass and provide alternative fodder. To assess the contribution of this diet-selection mechanism to inconsistent responses by plant species, we tested the following proposition: that the relative abundance of species of equal or higher palatability than the target species would be substantially less where the target species was classified D than where the target species was classified I.

Comparison of available highly preferred forage required abundance data. To avoid data incompatibility among studies, the data set was restricted to the eight grazing gradients of Landsberg *et al.* (1997b). These were grazed almost exclusively by sheep (Table 1). Abundances were frequencies from 80 quadrats of 1 m². Rankings of species' palatability to domestic grazers were assessed from the literature. Key-words and phrases were drawn from species' descriptions (Cunningham *et al.* 1992; Mitchell & Wilcox 1994; Wheaton 1994), see Appendix 2. These phrases were scored from high (1) to low (5) palatability by a sample of 13 ecologists. The mean score (rounded off) corresponding to the key-word or phrase was used to rank

species (Appendix 2). A pairwise approach was used. The differences between alternative forage (sum of abundances of species of equal or higher palatability) for increaser and decreaser cases of each of the ID species was calculated.

No significant difference was found between the relative abundances of alternative forage between increaser and decreaser cases of ID species (pairwise difference $t = 1.25$, d.f. = 47, $P = 0.22$). Hence, we found no support for the idea that differences in the availability of alternative forage were an important source of inconsistent responses.

Grazing intensity and response shape

Species often show abundance responses along a gradient of grazing intensity that are not monotonically increasing or decreasing, for example first increasing, peaking at some intermediate level and then decreasing at higher grazing intensities (Dyksterhuis 1949; Hacker 1987; Noy-Meir, Gutman & Kaplan 1989; Fensham, Holman & Cox 1999). For such species, comparisons between low and moderate grazing would show an opposite response to comparisons between moderate and high grazing. Might differences in grazing intensity have been an important source of inconsistencies among different studies? We did not find it possible to approach this question by defining particular grazing studies as having been conducted at higher vs. lower grazing intensity. However, within some studies, responses could be defined as being either (i) monotonic or (ii) peaked or troughed functions of grazing intensity.

We tested the proposition that, if a species was inconsistent (ID), then peaked or troughed responses should make up a greater proportion of the minority cases and fewer of the majority cases, while monotonic responses should be a greater proportion of majority cases and lesser proportion of minority cases. We found no evidence (Table 3) that peaked or troughed grazing responses were more prevalent in minority cases.

Grazing animal

Sheep tend to be more selective than cattle, choosing diets higher in protein and lower in grass (Wilson & Harrington 1984). To assess how much inconsistency might have resulted from different grazers, we used a contingency table approach with two variables: grazer and response. Cumulative responses across species were used, as no species had enough responses for testing alone. For each plant species, we first determined the baseline response (I or D) and the major grazer that elicited that response. Then we asked the question, would the opposite grazer elicit the opposite response? The data were sorted in two alternative ways, using the following rules. **1.** The most numerous combination of grazer by response was defined as the baseline case.

Either 2a. If there were two or more combinations

Table 3. Categorization of species' responses to different grazing intensities. Numbers (and proportions of row totals) of monotonic vs. peaked or troughed responses to grazing intensity for plant species that showed inconsistent responses (ID) among different response lists from Australian grazing studies. Note that species were only defined as monotonic in studies where the data gave sufficient resolution that it was possible for them to have been defined as peaked or troughed. Consequently, many responses were undefined as either monotonic or peaked or troughed. Minority response is whichever of the number of increaser (I) and decreaser (D) responses recorded for a species was smaller. If differences in grazing intensity among studies were an important source of inconsistency, then peaked or troughed responses should make up a greater proportion of the minority cases and fewer of the majority cases, while monotonic responses should be a greater proportion of majority cases and lesser proportion of minority cases

	Decreased relative abundance in response to grazing				Increased relative abundance in response to grazing			
	Troughed	Monotonic	Undefined	Total	Peaked	Monotonic	Undefined	Total
Minority response	1 (0.03)	18 (0.55)	14 (0.42)	33	10 (0.16)	36 (0.57)	17 (0.27)	63
Equal number of I and D	2 (0.03)	49 (0.64)	25 (0.33)	76	12 (0.16)	45 (0.58)	19 (0.25)	76
Majority response	6 (0.04)	109 (0.70)	41 (0.26)	156	16 (0.20)	50 (0.60)	16 (0.20)	82
Total	9 (0.03)	176 (0.66)	80 (0.30)	265	38 (0.17)	131 (0.59)	52 (0.24)	221

Table 4. Contingency table of grazer by response for species that increase or decrease in response to grazing. Responses have been summed across 55 species that had responses to both cattle and sheep and included both species with inconsistent (ID) and consistent responses. In this version, the baseline grazer was defined as the one for which most responses were available, not as the one for which responses were most consistent

	Baseline response	Opposite response	Total
Baseline grazer	105	30	135
Opposite grazer	46	24	70
Total	151	54	205

Table 5. Contingency table of grazer by response for species that increase or decrease in response to grazing. Responses have been summed across 55 species that had responses to both cattle and sheep and included both species with inconsistent (ID) and consistent responses. In this version, the baseline grazer was defined as the one for which responses were most consistent

	Baseline response	Opposite response	Total
Baseline grazer	105	18	123
Opposite grazer	46	36	82
Total	151	54	205

equally most numerous, then a baseline response was defined by the sum of responses to cattle and sheep. Then the most numerous grazer defined the baseline and opposite grazer cases.

Or 2b. Alternatively, where two or more combinations were equally most numerous, then the baseline grazer was defined as that for which the response was more consistent.

3. If there were equal numbers of I and D cases then either response was the baseline.

The data set was restricted to studies grazed by either sheep or cattle but not both. Species were rejected from

the data set if they did not have responses recorded to both cattle and sheep. Only I and D responses were used. Including both inconsistently (ID) and consistently responding species, 205 responses from 55 species made up the data set. Responses were summed over species to yield a contingency table of cumulative baseline and opposite responses by baseline and opposite grazers (Tables 4 and 5).

Considering first Table 4 (baseline grazer defined as the one with most responses available): if a range manager knew the baseline response of a plant species and the most numerous grazer, then went to a paddock grazed by the opposite animal, with what probability would the opposite response have been found? The answer was about one-third; $P(\text{opposite response} | \text{opposite grazer}) = 24/70 = 0.34$. This was detectably higher than the probability that the same (baseline) grazer would induce an opposite response [$P(\text{opposite response} | \text{baseline grazer}) = 30/135 = 0.22$; $G_{\text{adj}} = 3.34$, d.f. = 1, $P < 0.075$; with Williams' correction (Sokal & Rohlf 1995: 729)]. However it does not represent a very large increase in the capacity to predict opposite responses, and indeed the baseline response remained more likely ($P = 0.66$) even with the opposite grazer.

Considering Table 5 (baseline grazer defined as the animal that elicited more consistent responses) naturally led to a stronger association between grazer and response (Table 5). If a range manager was concerned with a species that responded most consistently in one direction to grazing by one animal, then the likelihood of the species responding in the opposite direction under the other grazer was over two-fifths; $P(\text{opposite response} | \text{opposite grazer}) = 36/82 = 0.44$ (Table 5), compared with a probability of $18/123 = 0.15$ of the opposite response under the baseline grazer. The increased chance of opposite response under non-baseline grazer could be measured by $G_{\text{adj}} = 21.31$, d.f. = 1, $P < 0.001$. However, the significance test should not be taken literally given that, under the rules for allocating cases, it was impossible to satisfy a null hypothesis that grazer made no difference to response.

Table 6. Australian rangeland plant species that showed different responses to cattle and sheep grazing. Twenty strongest response patterns shown. I = increase, D = decrease, S = sheep grazing, C = cattle grazing, number is responses

	Decreasers under sheep and increasers under cattle					Decreasers under cattle and increasers under sheep			
	DS	DC	IS	IC		DS	DC	IS	IC
<i>Aristida contorta</i>	2	1		3	<i>Panicum decompositum</i>	1	2	1	
<i>Brachyachne convergens</i>	1			2	<i>Abutilon otocarpum</i>	1	1	2	
<i>Monachather paradoxus</i>	2			1	<i>Acacia aneura</i>	1	1	2	
<i>Rostellularia adscendens</i>	1			2	<i>Ptilotus obovatus</i>	1	1	2	
<i>Solanum quadriloculatum</i>	2			1	<i>Themeda triandra</i>	3	4	1	
<i>Panicum effusum</i>	2		1	1	<i>Atriplex stipitata</i>		1	1	
<i>Enneapogon cylindricus</i>	1			1	<i>Crotalaria dissitiflora</i>		1	1	
<i>Senna artemisioides artemisioides</i>	1			1	<i>Digitaria coenicola</i>		1	1	
<i>Swainsona campylantha</i>	1			1	<i>Eremophila gilesii</i>		1	1	
<i>Chenopodium melanocarpum</i>	3	1	1	1					
<i>Tragus australianus</i>	1	1	1	3					

Cattle and sheep were not distributed evenly over the range of abiotic variables and this confounded the analysis somewhat. In particular, sheep were not present at sites of high summer rainfall. In summary, trials with opposite grazers were somewhat more likely to produce opposite responses than trials with the same grazer, but predictive power was still less than 1-in-2 under any definition of baseline. Species that displayed some difference in their responses to different grazing animals are listed in Table 6. Few species showed strong patterns of opposite response.

Discussion

This study assessed what limits there might be to generalizing from empirical grazing studies. Grazing responses are reported for Australian rangeland plant species but there seems no reason to expect outcomes to be different on other continents. More than one-third of species responded inconsistently to grazing, increasing in some situations and decreasing in others. However, species could not be divided into those that behaved consistently and those that behaved inconsistently. Rather, most features of the data could be understood if, for each species, about 1-in-4 of all responses went in the opposite direction to the majority response. Thus, it was quite common for species that had been studied two or three times to show consistent responses, but no species studied eight or more times was wholly consistent in its responses. Of course, it is unlikely that the probability of minority responses is identical across all species. Nevertheless, there was only limited evidence for higher or lower levels of consistency, rather a continuum, and many features of the data could be understood by assuming a common probability of minority response across all species.

Noy-Meir, Gutman & Kaplan (1989) also found inconsistency in grazing responses at 15 fenceline contrasts in Mediterranean grasslands. This allowed a comparison of response inconsistency. Applying the previously described analysis (equation 1 and Fig. 2) to the data from Noy-Meir, Gutman & Kaplan (1989), we

found that the incidence of at least one inconsistent response indeed increased with the number of occurrences. Similarly, the expected proportion of inconsistent species using the binomial model fitted the data observed by Noy-Meir, Gutman & Kaplan (1989) but with a mean probability of minority responses across all species and occurrences of $p = 0.107$. There are biologically meaningful reasons that might explain why this probability is lower than that in the present study ($p = 0.275$). The sites were all within 10 km radius, the same methodology was used and the recording was roughly concurrent (Noy-Meir, Gutman & Kaplan 1989).

This comparison suggests that the probability of minority responses is scale-dependent. As the geographical scale increases, species are exposed to a wider range of environmental conditions and a larger pool of co-occurring species. This should lead to a higher level of minority responses. However, the prediction of these responses should become more tractable as the range of case-specific variables increases. The question arises, do abiotic variables become more important and biotic variables less important with increasing scale?

Noy-Meir, Gutman & Kaplan (1989) also found one-third of 73 species responded inconsistently to grazing in their Mediterranean grasslands data. Comparing the consistent response groups from these three studies – present study excluding data of Landsberg *et al.* (1997b) (P), Noy-Meir, Gutman & Kaplan (1989) (N-M) and understorey data of Landsberg *et al.* (1997b) (LU) – is instructive. Percentages of consistent decreaseers were highest for LU (43%), then P (26%) and lowest for N-M (12%). Consistent increaseers followed the opposite trend: N-M 42%, P 34%, LU 11%. This could be explained by the long history of domestic grazing in Mediterranean grasslands [5000 years; Noy-Meir, Gutman & Kaplan (1989)]. By comparison, grazing pressure in Australia has increased enormously since European occupation (about 200 years ago), due largely to increased availability of water to domestic, native and feral grazers (James, Landsberg & Morton 1999). Additionally, Landsberg *et al.* (1997b) made an effort

to include water-distant reference sites that had very low levels of current and historical grazing. This differs from the situation for most of the other studies summarized here, which were generally more likely to have been grazed historically. Extremely sensitive species may have already disappeared from the bulk of the studies summarized here (Moore 1973).

Liberal assignment of responses, for example through criteria such as doubling in one paddock relative to another or by using trends across time or grazing intensity, may have led to a small increase in the incidence of inconsistency. While this subjectivity is undesirable in the sense of experimental ecology, the great majority of rangeland grazing studies are neither designed nor analysed optimally. The challenge is how to use the information that does exist effectively. The method we have used is closest to vote-counting. However, instead of the repeated trials nature of vote-counting proving a problem (Hedges & Olkin 1980; Gurevitch & Hedges 1999), we have explicitly used it to inform us about the likelihood of species response consistency.

Realizing that inconsistency lay among cases rather than within species allowed us to examine some case-specific variables to explain the responses. Species tended to be decreaseers where environmental conditions were suboptimal. Species were more likely to increase in response to grazing at higher rainfall sites and decrease at lower rainfall sites than vice versa. This is in general agreement with the range succession model where grazing and aridity are seen as complementary forces opposing succession (Stoddart, Smith & Box 1975). Forbs were more likely to be grazing increaseers at sites where rain fell predominantly in the cooler season. Forb species in Australia mostly respond to winter more than to summer rainfall (Harrington *et al.* 1984). Swapping the grazing animal did increase the probability of producing an opposite response, but the probability remained below 50%. Although this analysis was somewhat confounded by abiotic differences, we feel the result gives us little confidence in switching grazers as a reliable method for manipulating botanical composition.

The availability of alternative forage was not an important determinant of response direction. However, the abundances used for this model were means across grazing gradients (Landsberg *et al.* 1997b). This may have obscured differences between alternative forage for increaseer and decreaseer cases, compared with the ungrazed vegetation. As the most palatable forage is eaten from a paddock, the relative palatability of a species would increase, though more so for species low in the palatability rank (increaseers) than for species high in rank (decreaseers). Thus, any pattern of difference in alternative forage between increaseer and decreaseer cases would be diminished as grazing intensity increased.

A number of studies have shown unimodal species' responses to grazing intensity (Hacker 1984, 1987; Fensham, Holman & Cox 1999). Noy-Meir, Gutman & Kaplan (1989) found that, in a number of cases,

inconsistent grazing responses were congruent with unimodal responses common to a variety of ecological gradients. The data available here were not sufficient to shed any further light on this as unambiguous comparisons of grazing intensity could not be made, although it is possible that this contributed to inconsistent grazing responses.

The work reported here was originally planned as a precursor to relating increaseers and decreaseers to species' traits. However, what has emerged from the many years of research invested in grazing studies is that species cannot be labelled as wholly consistent increaseers or decreaseers. The implication is that prediction from traits of the species alone will necessarily fall short of 100% reliability. It must be the case that different outcomes for the same species are caused by features of the context, such as the other plant species present, the physical environment, the grazing animal, or combinations of features. To the extent made possible by the available data, we have investigated the potential for predicting inconsistent grazing responses from context information. This has had some limited success, but still falls well short of 100% reliability.

It would be wrong, however, to interpret a degree of inconsistency as meaning that rangelands research has produced no useful knowledge about botanical responses to grazing. There does appear to be a clear predominance of either increasing or decreasing under grazing for many species, and four to five studies should suffice to identify this direction, allowing for the chance of a minority response in any one study. It may be hoped that improved understanding of influences from the context, together with more detailed information about context, may bring predictive capacity closer to 100%. Experiments that deliberately seek to generate opposite responses in different situations will be powerful tools for advancing understanding of the inconsistencies.

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Supplementary material

The following material is available from <http://www.blackwell-science.com/products/journals/suppmat/JPE/JPE646/JPE646sm.htm>

Appendix 1. Species that occurred in at least two grazing response lists and their responses in those lists.

Appendix 2. Palatability ranking of key-words and phrases from species' descriptions in the literature.

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