Rangeland Ecol Manage 64:196–207 | March 2011 | DOI: 10.2111/REM-D-10-00062.1

Influence of Grazing Management on Plant Diversity of Highland Sourveld Grassland, KwaZulu-Natal, South Africa

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Abstract

Commercial livestock production offers one of the main opportunities for mainstreaming of biodiversity conservation in the grassland biome of South Africa. Grazing management is expected to influence success. With the uses of three long-term grazing trials, effects of stocking rate and cattle-to-sheep ratio on the plant composition and diversity of Highland Sourveld grassland in KwaZulu-Natal were examined. Plant diversity was sampled with the use of modified Whittaker plots. Canonical correspondence analysis was used to test the effects of treatments on compositional variation, and general linear models were used to test individual species' responses. In a biennial rotation, burned/grazed plots supported lower species richness of forbs and all plants than unburned/ungrazed plots, attributed to the impact of grazing during the season of occupation. A high stocking rate resulted in a long-term decrease of forb richness in one experiment, but an increase in another. An increasing proportion of sheep to cattle resulted in a long-term decrease of the richness of forbs and of total species richness. The three trials identified nongrass species that behaved as increasers or decreasers in response to an increase in stocking rate, and a set of species that behaved as decreasers in response to an increasing proportion of sheep to cattle. Constraints on using long-term trials for identifying the effects of livestock management on plant diversity include lack of baseline data, limited replication, pre-experimental impacts on the study site, and the difficulty of assessing uncommon species.

Resumen

La producción ganadera comercial ofrece una de las principales oportunidades para canalizar la conservación de la biodiversidad en los pastizales de Sudáfrica. Se espera que el manejo del pastoreo influya en tener éxito. Con este fin, se evaluó el uso de tres ensayos de pastoreo a largo plazo, el efecto de la carga animal y la relación de ganado-ovejas en la composición y diversidad de los pastizales en Highland Sourveld grassland KwaZulu-en Natal. La diversidad de plantas fue muestreada utilizando la técnica modificada de las parcelas de Whittaker. Análisis de correspondencia canónica fueron utilizados para probar los efectos de los tratamientos sobre la variación de la composición, y los modelos lineares generales fueron usados para probar la respuesta individual de las especies. En una rotación bienal las parcelas quemadas/pastoreadas presentaron el menor número de especies de herbáceas y de todo tipo de plantas, comparadas con las parcelas sin quema y/o pastoreo. Esto se atribuyó al impacto de la actividad de pastoreo durante la época en que se llevó a cabo. Una mayor carga animal dio como resultado una disminución a largo plazo de la riqueza de herbáceas en un experimento pero se incrementó en otro. Al incrementarse la proporción de ovejas sobre el ganado hubo una disminución a largo plazo sobre el número de herbáceas, así como una disminución en el número total. Durante los tres estudios se identificaron especies no gramíneas cuyo comportamiento fue de incremento o disminución en respuesta al aumento en la carga animal. Asimismo, se observó un grupo de plantas que disminuyeron en respuesta al incremento en la proporción de ovinos sobre bovinos. Las restricciones sobre el uso de ensayos a largo plazo para la identificación del efecto del manejo del ganado en la diversidad de las plantas incluyen la carencia de datos iniciales, limitación en las repeticiones, impacto pre-experimentales del sitio de estudio, y la dificultad de evaluar especies pocos comunes.

Key Words: grazing experiment, increaser–decreaser classification, mixed grazing, species richness, stocking rate

INTRODUCTION

Less than 2% of South Africa's grassland biome has been set aside as protected area (Reyers and Tosh 2003). Competing land-use demands are likely to preclude a significant increase in this area, such that mainstreaming biodiversity conservation

Research was funded in part by the National Research Foundation.

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Manuscript received 12 April 2010; manuscript accepted 9 December 2010.

within other land uses is being pursued (Pierce et al. 2002; Petersen and Huntley 2005). This biome supports in excess of 10 mainland uses that differ markedly in their impact on its biodiversity integrity (O'Connor and Kuyler 2008). Commercial livestock ranching is the most important land use for mainstreaming biodiversity conservation in the grassland biome because it is relatively biodiversity friendly and because it comprises more than 50% of the biome's area (Anon 2010). Approaches to livestock ranching can be diverse in terms of animal and grassland management (Tainton 1999), raising the question of which management variables are most important for maintaining biodiversity integrity. The main variables for livestock management are animal type, stocking rate, and grazing system, whereas fire is the most important variable for vegetation management.

South African grasslands have enjoyed a long history of research addressing the relationship between livestock management variables and the grassland resource that has concentrated on composition and production of grasses (Tainton 1999). Although grazing pressure (stocking rate) is known to impact on grassland plant diversity in South Africa (O'Connor 2005; Uys 2006) and elsewhere (Milchunas et al. 1988; Milchunas and Lauenroth 1993; McIntyre et al. 2003), a review of South African research failed to locate a single study that had directly examined the effect of livestock management variables on plant diversity (O'Connor et al. 2010). This dearth of insight is not unique to South Africa—a recent review of US research (Briske et al. 2008) identified only one directly relevant study (Hickman et al. 2004). Long-term grazing experiments offer an opportunity for redressing this deficiency.

A degree of prediction of responses of plant diversity to livestock grazing may be possible through comparison with responses of grass composition and richness, which has been relatively well studied (Tainton 1999). However, the graminoid growth form is adapted to trampling and grazing (Briske and Richards 1995) whereas most nongraminoid growth forms are not (Uys 2006). In southern African grassland, stocking rate has consistently been identified as a key variable, and small-bodied sheep generally have a greater impact on grass composition than cattle owing to their ability to graze closely, but this depends on stocking rate (O'Reagain and Turner 1992). The response of individual grass species to grazing pressure depends on their attributes. Sustained grazing pressure usually results in a decline, or even local extirpation, of long-lived, palatable species (O'Connor 1991) and increases of short-lived species and those that can avoid or tolerate grazing (Briske and Richards 1995). A preliminary expectation therefore is that an increase in the ratio of sheep to cattle, or of stocking rate of either, may impact the composition and possibly richness of the nongraminoid component of grassland. Sheep in particular should have a greater impact than cattle because they include more forbs in their diet (Owen-Smith 1999). Terrain can modulate the impact of grazing through both effects on accessibility and ease of foraging and through indirect effects of increased soil erosion resulting from grazing of slopes (Venter et al. 1989; Fynn and O'Connor 2000).

The aim of this study was to examine the influence of stocking rate and cattle-to-sheep ratio on the botanical composition and richness of species-rich grassland, with the use of long-term grazing trials established in the Highland Sourveld grassland of KwaZulu-Natal, South Africa.

METHODS

Study Area

The study was conducted at the Kokstad Agricultural Research Station in KwaZulu-Natal (lat 30°31′S, long 29°25′E). Mean annual rainfall at station headquarters is 790 mm, falling mainly during the summer months of September–April. Coefficient of variation of rainfall is 19.8%, indicating that the influence of interannual variation of rainfall on vegetation changes should not be marked. Rainfall for the 2003/2004 season of 505 mm was, however, the lowest on record, but its effect cannot be assessed. The growing season from September to April is on average warm, with a mean daily maximum of 24.5°C, whereas the winter period from May to August is cool, with a mean daily minimum of 2.1°C, and frost occurs frequently. Topography includes both steep hills and undulating lowlands. Altitude ranges from 1 340 to 1 650 m above sea level across the experimental portion of the research station. Soils are derived from Karoo sandstones and dolerite intrusions. The lower, undulating portion of the station supports 90–120-cm deep, well-drained soil of mainly the Hutton and Clovelly forms (Short 2010). Steep slopes support 30–90-cm deep soil of mainly the Hutton, Clovelly, and Mispah forms. All soils displayed a luvic B-horizon, which indicates a higher clay content than is found in the A or E horizons. Vegetation is classified as GS12-East Griqualand Grassland (Mucina and Rutherford 2006), originally known as Highland Sourveld (Acocks 1953). The vegetation is short, tufted grassland dominated by *Themeda triandra* and *Tristachya leucothrix*, and is rich in nongraminoid species. Plant nomenclature follows Germishuizen and Meyer (2003).

Experiments

Three long-term grazing trials were used. The Simulation trial, established in 1989, simulated a four-paddock rotational grazing system, which has one paddock rested for the growing season and the other three grazed rotationally by livestock according to a fixed schedule of 2 wk in and 4 wk out. To minimize land requirements, only one of the four paddocks was established per treatment combination. Livestock used adjacent rangeland during their 4-wk period out of the paddock. Experimental variables were stocking rate and cattle-to-sheep ratio. The two intended stocking rates were 1.0 and 0.5 animal units (AU, defined as a 450-kg steer following Meisnner 1982) per hectare, but in practice the mean stocking rate varied between 0.59 and 0.73 and 0.90 and 1.47 $AU \cdot ha^{-1}$ for low and high stocking treatments, respectively. Five ratios of cattle to sheep, based on AU, were used: 1:0, 3:1, 1:1, 1:3, and 0:1. The animals used were yearling Hereford or Nguni steers and two-tooth merino hamels (castrated males). All combinations of stocking rate and cattle-to-sheep ratio were used, but with no replication, to result in 10 paddocks in total (average paddock size of 0.75 ha). Grazing intensity was accidentally increased to 2 wk in and 3 wk out between 1998 and 2004. A rested paddock was burned in early spring of the season of rest and again the following spring. The paddocks were rested in the 2000/2001 and 2004/2005 seasons, but the rest cycle was omitted by accident in the 1996/1997 season. The trial was situated on a gentle slope (4–12%) of the undulating lowland region.

Two separate two-paddock trials were established to investigate the effect of stocking rate of sheep. For each trial, one paddock of each replicate was rested for the entire growing season. The other paddock of each replicate was burned after the first spring rains (usually September), stocked shortly thereafter, and stocked continuously for the growing season (usually ending in April). In the following year, the rested paddock was burned and grazed, and the previously grazed paddock was rested. One trial was established in 1992 on lowland grassland. Stocking rate was one or two $AU \cdot ha^{-1}$ for the season of grazing, each on two different slopes (4% and 13%), to result in a total of eight paddocks. Another was established in 1996 on a steep (20%), west-facing slope. Stocking-rate treatment for the season was 1.0, 1.5, or 2.0 $AU \cdot ha^{-1}$ for the season of grazing, with each replicated twice, to result in a total of 12 paddocks. Experimental animals for the two-paddock trials were weaned merino lambs; hamels were stocked on the lowland and ewes on the hill-slope site. Paddocks were between 0.25 and 0.55 ha in size. Note that the long-term stocking rate is half that of the values stated above because one of the two paddocks is rested each year. Paddocks were completely randomized on the hill-slope trial, whereas the two paddocks were immediately adjacent to one another (and grazed in alternate years) on the lowland trial.

Vegetation Sampling

Plant diversity and species composition of each paddock were sampled with the use of a modified Whittaker plot (Stohlgren et al. 1995), but excluded the 100-m^2 plot within the 1 000-m^2 plot because it is inefficient for this vegetation type (O'Connor 2005). This design samples vegetation within an area of 20 × 50 m, with the long axis aligned with the apparent gradient of maximum vegetation turnover. For each plot, 20 1-m^2 quadrats were sampled along the long-axis boundary, and a 10-m^2 quadrat was sampled in two diagonally opposite corners. Smaller quadrats were not nested within larger quadrats in order to ensure spatial independence (Stohlgren et al. 1995). For each 1-m^2 quadrat, every species was recorded and its aerial cover was estimated with the use of the Domin scale (Jager and Looman 1987). A voucher specimen of each species was collected for checking of species identification by herbaria of the University of the Witwatersrand, South African National Biodiversity Institute, and Ezemvelo KZN Wildlife. Vegetation sampling was conducted during December 2005 for the simulation trial and two-paddock trial on a hill slope, and during December 2006 and January 2007 for the lowland two-paddock trial.

Data Analysis

The variables of primary interest in all analyses are the effects of livestock management variables, specifically stocking rate and cattle-to-sheep ratio. Other management or topographical effects need to be accounted for because they may potentially obscure such effects.

For each trial, canonical correspondence analysis (CCA), a direct gradient analysis technique, was used to examine whether management variables accounted for the pattern of compositional variation, using the CANOCO 4.5 package (Ter Braak and Smilauer 2002). The community data set excluded uncommon species. Owing to the effect of grazing on cover abundance, percentage frequency was deemed to be a more stable measure of species representation. The environmental data set depended on the trial in question. For each of the two-paddock trials, the environmental variables were stocking rate and whether the paddock had been burned during the 2005/2006 season or not. In addition for the two-paddock trial on the hill slope, an apparent pediment effect of material and moisture redistribution down the slope was accommodated by creating a dummy pediment variable. (Following preliminary analysis, it was considered unnecessary to include slope in the analysis of the two-paddock lowland site.) The model fitted was the three main effects and the interaction between stocking rate and burning/grazing. For the simulation trial, stocking rate and cattle-to-sheep ratio was fitted, but an interaction term was not included because of absence of replication. Significance of the first axis and of the ordination overall was tested with a Monte Carlo permutation test (199 permutations).

Indices used to describe plant diversity were species richness (m^{-2}); Shannon-Weiner diversity, calculated with the use of cover scores as $H' = \sum p_i \ln p_i$, where p_i is the proportion of the total sample accounted for by the ith species ($i = 1$ to s); and evenness, calculated as $J' = H'/H_{\max}$. Differences among treatments were examined with a general linear model (Type III sums of squares) and means compared with Tukey's test, with the use of SAS (2002/2003). Variables analyzed were H', J', richness of graminoids, nongraminoids (forbs), and of all species, plus frequency of occurrence (within the 20 1-m^2 quadrats) of individual species with the use of arcsine-transformed data. H' and J' are not discussed further because no meaningful results were obtained. The models tested were the same as for the CCAs. Owing to limited replication within each field trial, $P < 0.05$ was considered a strong effect and $0.05 < P < 0.1$ a significant effect. The increased probability of a false significant response when testing so many species was not considered relevant to the purpose of these analyses.

RESULTS

Simulation Trial

A total of 113 species were recorded on the simulation trial, of which 30 were grasses, 20 were Asteraceae, and the remainder were spread across 29 other families. The dominant grass species across all treatments except one was *T. triandra,* with *Alloteropsis semialata* and *Microchloa caffra* also abundant (Table 1). *Microchloa caffra* was the most abundant species of the high stocking level grazed by sheep only.

The CCA indicated that stocking rate and cattle-to-sheep ratio accounted for compositional variation along the first axis ($F = 1.766$, $P = 0.024$) and for the ordination overall ($F = 1.56$, $P = 0.014$). Axis 1 was defined primarily by stocking rate, and axis 2 was defined by cattle-to-sheep ratio whose effect was relatively independent of that of stocking rate (Fig. 1, Table 2). The species whose variance was well accounted for by the CCA

Table 1. The nine most abundant species by aerial cover (%) of each treatment for (a) simulation trial, (b) two-paddock trial on hill slope, and (c) two-paddock trial on lowland (top three species shown in bold typeface).

Table 1a. Simulation trial.

	Low stocking rate: Cattle-to-sheep ratio					High stocking rate: Cattle-to-sheep ratio				
Species	1:0	3:1	1:1	1:3	0:1	1:0	3:1	1:1	1:3	0:1
Themeda triandra	**16.3**	**9.9**	**18.4**	**19.4**	**11.7**	**6.3**	**8.3**	**29.0**	**21.8**	**3.0**
Alloteropsis semialata	**2.1**	**2.4**	**1.9**	**3.0**	**7.5**	0.9	0.8	**0.8**	**3.6**	**7.0**
Microchloa caffra	0.3	1.1	0.4	**1.5**	**1.9**	1.3	**2.1**	0.3	1.3	**10.1**
Tristachya leucothrix	0.9	**2.5**	0.5	1.3	1.1	1.0	0.9	**0.8**	0.9	0.8
Elionurus muticus	**1.6**	2.0	0.4	0.7		**2.0**	0.8	0.5		
Senecio retrorsus	0.5	0.4	**0.7**	0.4	0.5	0.5	0.5	0.6	3.3	0.6
Eragrostis curvula		0.5				0.6	**2.6**		1.4	0.5
Sporobolus africanus							0.4	0.3	**4.0**	0.4
Pentanisia angustifolia	0.5					**2.1**				
Acalypha schinzii		0.5	0.5	0.3		0.5		0.5		
Abilgaardia ovata			0.2		0.3		0.5	0.3	0.4	0.3
Helichrysum nudifolium	0.4	0.6			0.3					
Bulbostylis oritrephes				0.4	0.6					
Diheteropogon amplectens			0.2	0.5						
Acalypha punctata	1.2									
Vernonia natalensis					0.5					
Eragrostis plana									0.4	0.2

Table 1b. Two-paddock trial: hill slope.

	Low stocking rate		Medium stocking rate		Heavy stocking rate	
Species	Burned/grazed	Unburned/ungrazed	Burned/grazed	Unburned/ungrazed	Burned/grazed	Unburned/ungrazed
Themeda triandra	**3.1**	**8.2**	**3.5**	**3.4**	**3.0**	**4.3**
Alloteropsis semialata	**4.5**	**5.0**	**3.7**	**5.7**	**5.2**	**2.9**
Diheteropogon filifolius	**11.4**	**38.2**	**17.3**	**38.8**	**18.5**	0.5
Heteropogon contortus		0.4				**1.1**
Senecio retrorsus	0.3	0.2	0.5	0.3		
Eragrostis curvula						0.7
Sporobolus africanus	0.3		0.4		0.5	0.6
Pentanisia angustifolia		0.3		0.5		0.8
Helichrysum nudifolium		0.3	0.3			
Acalypha punctata	0.5		0.3		0.3	
Vernonia natalensis	0.5		0.5			
Eragrostis plana					0.4	
Senecio speciosus						0.8
Scabiosa columbaria				0.3	0.3	0.4
Anthospermum herbaceum	0.3	0.4		0.3	0.3	0.4
Helichrysum herbaceum	0.5	0.5	0.4	0.4	0.3	
Panicum ecklonii				0.3		

were mainly those which exhibited a significant response in the general linear models. Of the 54 species tested, an increase in stocking rate promoted five graminoid ($P < 0.05$: *Eragrostis curvula*, $0.05 < P < 0.1$: *Abildgaardia ovata*, *Brachiaria serrata*, *Eragrostis plana*, *Sporobolus africanus*) and one forb (*Senecio retrorsus*, $P < 0.05$) species, but had an unfavorable effect on the occurrence of two graminoid ($P < 0.05$: *Eulalia villosa*, $0.05 < P < 0.1$: *Bulbostylis oritrephes*) and three forb ($P < 0.05$: *Helichrysum nudifolium*, $0.05 < P < 0.1$: *Oxalis smithiana*, *Pentanisia angustifolia*) species. A greater proportion of sheep resulted in a negative impact on the occurrence of five forb species ($P < 0.05$: *Commelina africana*, *Helichrysum nudifolium*, *Helichrysum pilosellum*, *Pentansia angustifolia*, $0.05 < P < 0.1$: *Ajuga ophyridis*), whereas cattle facilitated the increase of *E. curvula* ($P < 0.05$) under heavy grazing.

Species richness (m^{-2}) of all species and of nongraminoid species declined in relation to an increasing proportion of sheep, whereas a heavy stocking rate resulted in a lower number of forb species (Fig. 2; Table 3a).

Table 1. Continued.

Table 1c. Two-paddock trial: lowland.

Species	Low stocking rate		High stocking rate	
	Burned/grazed	Unburned/ungrazed	Burned/grazed	Unburned/ungrazed
Themeda triandra	**7.6**	**17.0**	**10.2**	**15.9**
Alloteropsis semialata	**3.2**	**4.9**	**1.6**	1.0
Microchloa caffra		0.7	0.7	0.8
Tristachya leucothrix	0.9	0.9	0.8	0.9
Heteropogon contortus			0.6	0.9
Elionurus muticus	**2.0**		**1.3**	**2.1**
Senecio retrorsus	0.5	**1.0**	1.0	0.8
Pentanisia angustifolia			0.5	1.0
Acalypha schinzii	0.7	0.8		0.9
Koeleria capensis	0.5	0.8	0.7	**1.1**
Helichrysum miconiifolium	0.6			
Hypoxis angustifolia	1.0	0.6		
Cyperus sphaerocephalus		0.7		

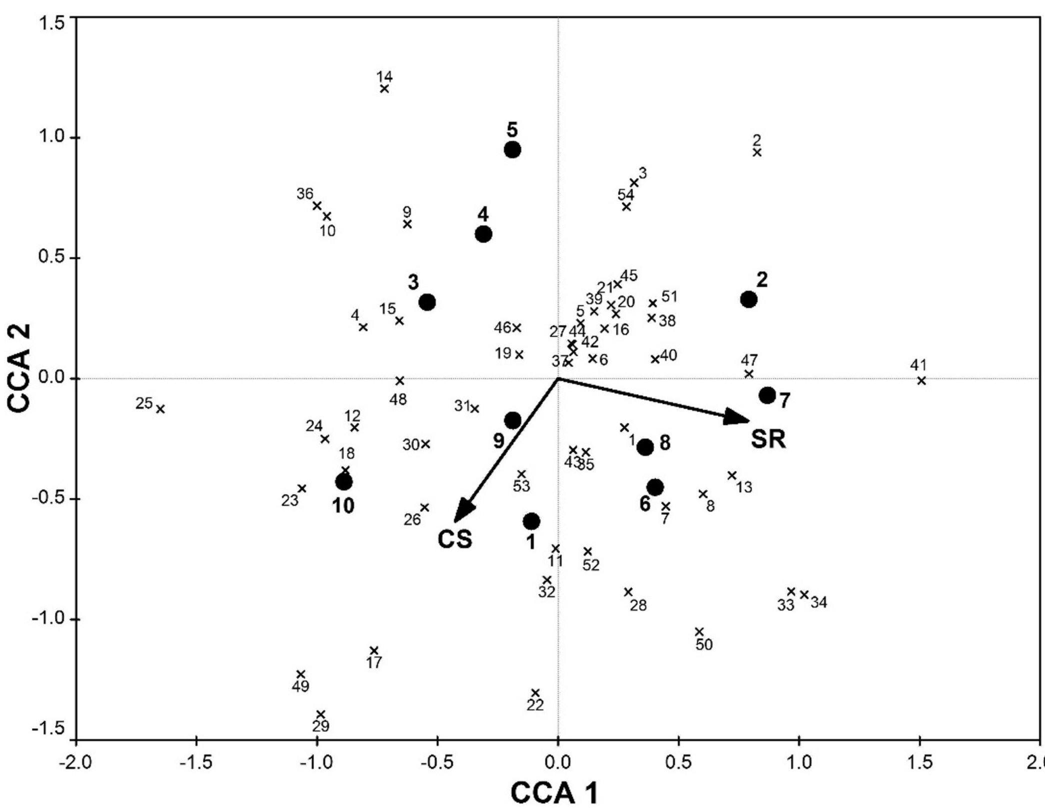

Figure 1. The first two axes of a canonical correspondence analysis for the simulation trial (see Table 2 for results). Key to variables: CS, cattle-to-sheep ratio; SR, stocking rate. Solid circles are individual plots. Key to species: 1, *Barleria* sp.; 2, *Helichrysum cephaloideum*; 3, *Helichrysum herbaceum*; 4, *Helichrysum nudifolium*; 5, *Helichrysum pilosellum*; 6, *Senecio retrorsus*; 7, *Sonchus nanus*; 8, *Tolpis capensis*; 9, *Vernonia natalensis*; 10, Asteraceae sp. 2; 11, *Cynoglossum hispidum*; 12, *Commelina africana*; 13, *Abilgaardia ovata*; 14, *Bulbostylis oritrephes*; 15, *Cyperus sphaerocephalus*; 16, *Scabiosa columbaria*; 17, *Acalypha punctata*; 18, *Acalypha schinzii*; 19, *Ledebouria ovatifolia*; 20, *Hypoxis argentea*; 21, *Hypoxis rigidula*; 22, *Ajuga ophrydis*; 23, *Hibiscus aethiopicus*; 24, Orchid sp.; 25, *Oxalis smithiana*; 26, *Raphionacme hirsuta*; 27, *Alloteropsis semialata*; 28, *Brachiaria serrata*; 29, *Digitaria tricholaenoides*; 30, *Diheteropogon amplectens*; 31, *Elionurus muticus*; 32, *Eragrostis capensis*; 33, *Eragrostis curvula*; 34, *Eragrostis plana*; 35, *Eragrostis racemosa*; 36, *Eulalia villosa*; 37, *Heteropogon contortus*; 38, *Koeleria capensis*; 39, *Microchloa caffra*; 40, *Setaria nigrirostris*; 41, *Sporobolus africanus*; 42, *Themeda triandra*; 43, *Trachypogon spicatus*; 44, *Tristachya leucothrix*; 45, *Polygala ohlendorfiana*; 46, *Anthospermum herbaceum*; 47, *Anthospermum rigidum*; 48, *Kohautia amatymbica*; 49, *Pentanisia angustifolia*; 50, *Diclis rotundifolia*; 51, *Graderia scabra*; 52, *Striga bilabiata*; 53, *Hermannia depressa*; 54, *Vernonia natalensis*.

Table 2. Summary of the canonical correspondence analysis output for the three experiments.

	Simulation trial			Two-paddock on hill slope			Two-paddock on lowland		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Eigenvalues	0.075	0.040	0.076	0.102	0.061	0.053	0.085	0.041	0.026
Species-environment correlations	0.969	0.920	0.000	0.968	0.927	0.913	0.956	0.978	0.957
Cumulative percentage variance									
Species data	20.1	30.8	51.2	22.7	36.3	48.1	26.9	39.7	47.9
Species-environment relation	65.4	100.0		42.3	67.6	89.6	56.2	83.0	100.0
Canonical coefficients									
Stocking rate (SR)	0.467	−0.244		−0.398	−0.071	0.255	−0.354	−0.310	−0.376
Cattle-to-sheep ratio	−0.139	−0.452							
Burn/graze (BG)				0.180	0.164	−0.134	0.386	−0.443	−0.301
SR•BG				0.366	−0.293	0.368	−0.180	0.118	0.650
Pediment				−0.155	0.478	0.146			

Two-Paddock Trial on Hill Slope

A total of 122 species were recorded on the hill-slope trial, of which 30 were grasses, 31 were Asteraceae, and 31 families represented the remainder. *Diheteropogon filifolius* was on average the dominant species, usually contributing more than 65% of aerial cover, with *T. triandra* and *Alloteropsis semialata* as lesser codominants (Table 1). *Diheteropogon filifolius* increased in abundance up the slope, thereby potentially obscuring grazing treatment effects.

The CCA confirmed that stocking rate, fire, and pediment had a significant effect on both the first axis ($F = 2.056$, $P = 0.008$) and on the overall ordination ($F = 2.029$, $P = 0.002$; Fig. 3, Table 2). The first axis was strongly constrained by burning/grazing and its interaction with stocking rate; that was opposite in effect to the influence of stocking rate. From its position in ordination space (Fig. 3), the pediment influence appeared relatively independent of the other two main effects and accounted for much of the variation along the second axis. The third axis described mainly additional variation in stocking rate and its interaction with burning/grazing. Thus the influence of stocking rate, which is the variable of interest, was obscured to some extent by the influence of pediment and burning/grazing. General linear models performed for 49 species confirmed that position in relation to pediment had strongly affected ($P < 0.05$) the occurrence of three species, and weakly influenced ($0.05 < P < 0.1$) that of a further seven species. A grass (*Poa binata*) and three forb (*Anthospermum herbaceum*, *Helichrysum aureum*, *Hermannia depressa*) species were less frequent on pediment, with the converse pattern shown by two grasses (*Eragrostis racemosa*, *Microchloa caffra*) and four forbs (*Diclis rotundifolia*, *Polygala ohlendorfiana*, *Scabiosa columbaria*, *S. retrorsus*). Burning and grazing during the survey year had resulted in a greater occurrence ($P < 0.05$) of the grass *Harpochloa falx* and four forb species (*Acalypha punctata*, *Helichrysum cephaloideum*, *S. columbaria*, *Vernonia natalensis*), but a decreased abundance of a grass (*Eragrostis curvula,* $0.05 < P < 0.1$) and four forbs ($P < 0.05$: *Graderia scabra*, *Hibiscus aethiopicus*, $0.05 < P < 0.1$: Asteraceae sp. 1, *Tolpis capensis*). Notwithstanding these two influences, an increase in stocking rate was associated ($P < 0.05$) with an increase of five forbs (Asteraceae sp. 1, *Ajuga ophrydis*, *P. angustifolia*, *S. columbaria*, *Senecio speciosus*), whereas one forb (*Senecio coronatus*) was most abundant at an intermediate level of stocking.

Richness (m^{-2}) of all species and of forbs was less if the plot had been burned and grazed during the season of sampling, whereas richness of grass species was unaffected (Table 3b). Fewer graminoid species occurred on the upper than the lower slope of the site. There was a clear influence of stocking rate despite the effects of fire and position in relation to pediment, in that a greater richness of forbs occurred under high than medium or low stocking rate.

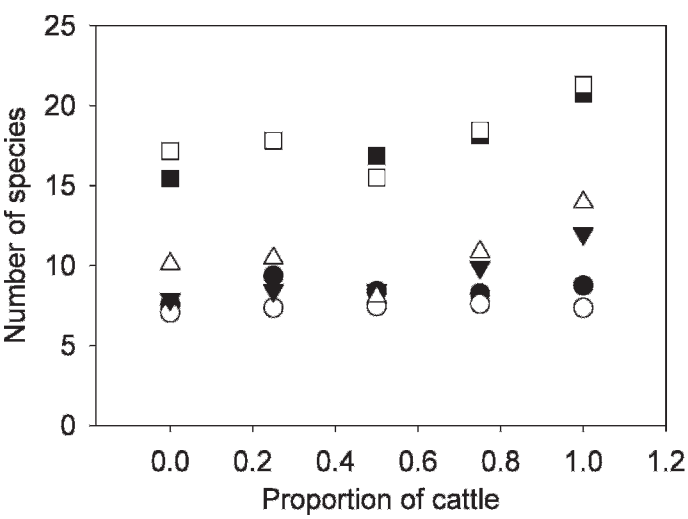

Figure 2. Mean number (m^{-2}) of graminoid (circle), forb (triangle), and total (square) species richness for the simulation trial. Open and closed symbols denote a light and heavy stocking rate, respectively.

Two-Paddock Trial on Lowland

A total of 130 species, including two exotics, were recorded on the two-paddock lowland trial, of which 27 were grasses, 23 were Asteraceae, and 29 from other families were represented. *Themeda triandra* was the dominant grass species across all treatments, with *Alloteropsis semialata*, *Elionurus muticus*, and *S. retrorsus* as codominants.

Table 3. Mean number of species (m^{-2}) for total, graminoid, and nongraminoid (forb) species (see Fig. 2 for simulation trial), and associated *P* values from general linear models (bold are significant at $P < 0.1$).

Variable	Number of species		
	Total species	Graminoid species	Forb species
(a) Simulation trial			
P stocking rate	0.6504	**0.0156**	**0.0510**
P cattle-to-sheep ratio	**0.0149**	0.3347	**0.0187**
(b) Two-paddock hill slope			
High stocking rate, unburned/ungrazed	18.325	6.60	11.725
High stocking rate, burned/grazed	14.70	6.325	8.375
Medium stocking rate, unburned/ungrazed	17.0	6.275	10.725
Medium stocking rate, burned/grazed	13.60	5.95	7.65
Low stocking rate, unburned/ungrazed	16.425	6.40	10.025
Low stocking rate, burned/grazed	14.30	7.075	7.225
P stocking rate (SR)	0.1591	0.3900	**0.0089**
P burn/graze (BG)	**0.0019**	0.6445	< **0.0001**
P SR • BG	0.4799	0.6821	0.5626
P pediment	0.6645	0.2096	0.1302
(c) Two-paddock lowland			
High stocking rate, unburned/ungrazed	23.025	8.875	14.15
High stocking rate, burned/grazed	17.35	7.55	9.80
Low stocking rate, unburned/ungrazed	21.675	9.15	12.525
Low stocking rate, burned/grazed	16.95	8.925	8.025
P stocking rate (SR)	0.6914	0.3529	0.2778
P burn/graze (BG)	**0.0642**	0.3797	**0.0309**
P SR • BG	0.8281	0.5224	0.9585

The CCA model provided a weak fit of stocking rate, burning/grazing and the interaction of these two effects along both the first axis ($F = 1.471$; $P = 0.164$) and the overall ordination ($F = 1.224$; $P = 0.228$; Fig. 4, Table 2), attributed in part to a small sample size. There was, however, a conditional effect for stocking rate ($F = 1.76$, $P = 0.086$). The effect of stocking rate, which was the main variable constraining the first axis, was relatively independent of that of burning/grazing, which accounted for much of the variation along the second axis. Of the 54 species analyzed, burning followed by grazing during the season of survey resulted in a reduction of three forb species ($P < 0.05$: *Anthospermum herbaceum*, *P. angustifolia*, $0.05 < P < 0.1$: *A. ophrydis*) and an increase ($0.05 < P < 0.1$) of one sedge (*Bulbostylis oritrephes*) and three forb species (*Albuca setosa*, *G. scabra*, *Ledebouria ovatifolia*). A high stocking rate had resulted in a decrease of two graminoids ($P < 0.05$: *A. semialata*, *B. oritrephes*) but had favored one grass ($P < 0.05$: *Setaria nigrirostris*) and four forb ($P < 0.05$: *P. angustifolia*, *S. columbaria*, $0.05 < P < 0.1$: *Gerbera ambigua*, *Rhynchosia totta*) species.

The pattern for species richness was similar to that for the two-paddock trial on the hill slope (Table 3c). Species richness (m^{-2}) of forbs, and hence total species richness, was higher on unburned/ungrazed than on burned/grazed plots. This was attributed to grazing having removed aboveground growth of certain species during that season, although stocking rate had no effect.

DISCUSSION

The Experimental Conundrum

Experiments are a tool of choice for advancing ecological understanding (Hairston 1989) but the limitations of field trials need to be recognized. A number of features were identified that were considered to have influenced the strength of conclusions. These trials were well designed as grazing trials, but replication for grazing trials is inevitably limited because of paddock size. Consequently, power of statistical tests is compromised. Furthermore, it is not realistic for grazing paddocks to meet the requirement of uniform experimental units at the commencement of a trial, as there will always be spatial variation in botanical composition. Natural variability across paddocks will tend to obscure treatment effects. This influence could have been accommodated by monitoring from the inception of an experiment, but unfortunately plant diversity was not an original objective for these production experiments.

An influence of burning/grazing on the composition of the two-paddock trials is an expected response because many nongraminoid species are cued to grow following fire, but to lie dormant under unburned conditions (Hilliard and Burtt 1987). However, burning/grazing resulted in lower species richness on the hill-slope experiment, possibly because its shorter sward (Short 2010) enabled more severe sheep grazing compared with the lowland site (Tables 3b and 3c), thus further obscuring

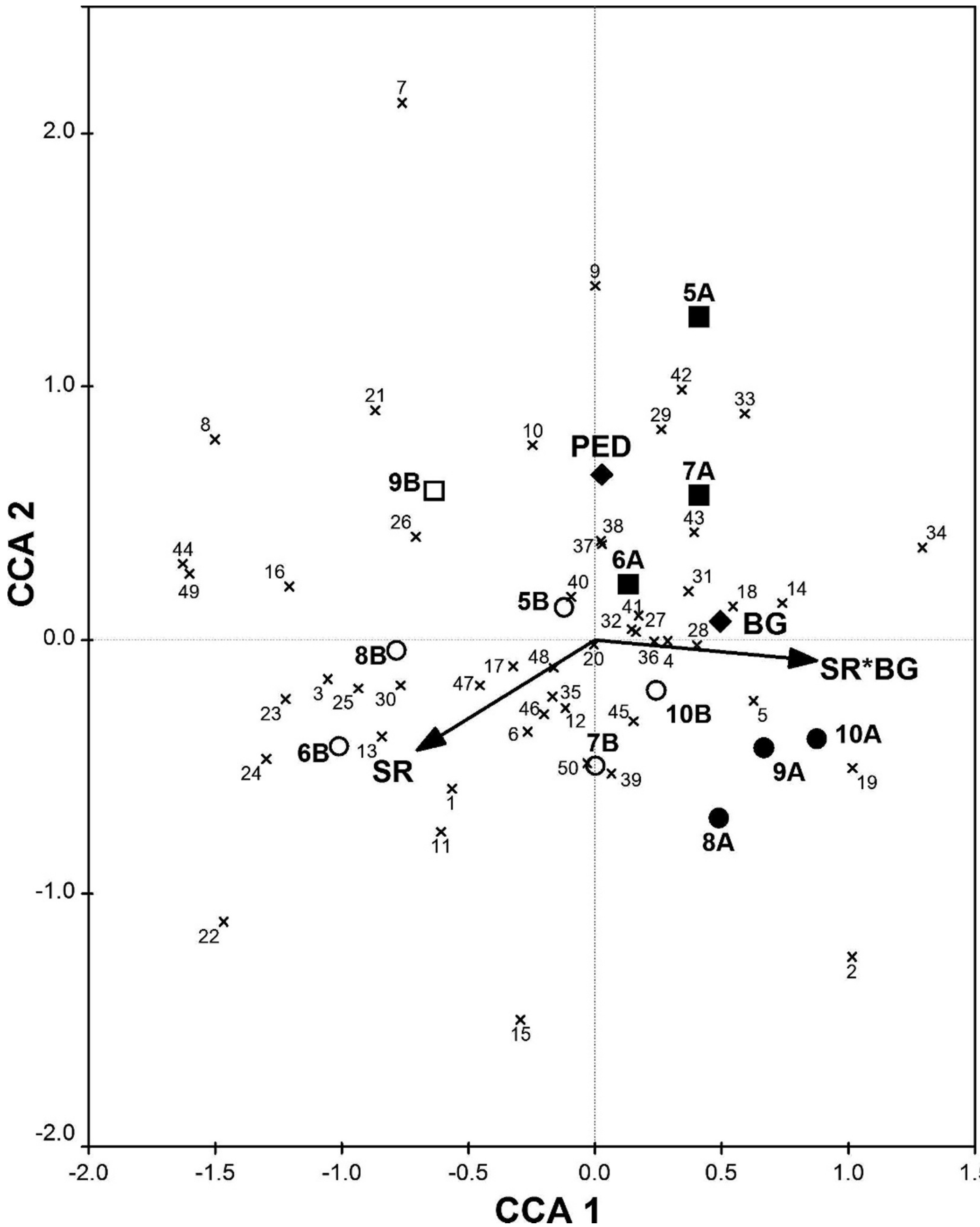

Figure 3. The first two axes of a canonical correspondence analysis for the two-paddock trial on a hill slope (see Table 2 for results). Key to variables: BG, burned/grazed (vs. unburned/ungrazed); PED, pediment slope; SR, stocking rate. Filled symbols indicate paddocks that had been burned/grazed during the season of sampling; open symbols indicate paddocks that had not. Squares indicate paddocks that are predominantly pediment; circles indicate paddocks on the upper portion of the slope. Key to species: 1, *Gerbera piloselloides*; 2, *Helichrysum aureum*; 3, *Helichrysum cephaloideum*; 4, *Helichrysum herbaceum*; 5, *Helichrysum nudifolium*; 6, *Helichrysum pilosellum*; 7, *Helichrysum thalypterum*; 8, *Senecio coronatus*; 9, *Senecio retrorsus*; 10, *Senecio scitus*; 11, *Senecio speciosus*; 12, *Sonchus nanus*; 13, *Tolpis capensis*; 14, *Vernonia natalensis*; 15, Asteraceae sp. 1; 16, Asteraceae sp. 2; 17, *Scabiosa columbaria*; 18, *Acalypha punctata*; 19, *Acalypha schinzii*; 20, *Monsonia angustifolia*; 21, *Hypoxis argentea*; 22, *Hypoxis gerrardii*; 23, *Ajuga ophrydis*; 24, *Stachys sessilis*; 25, *Hibiscus aethiopicus*; 26, *Oxalis smithiana*; 27, *Alloteropsis semialata*; 28, *Diheteropogon filifolius*; 29, *Eragrostis capensis*; 30, *Eragrostis curvula*; 31, *Eragrostis plana*; 32, *Eragrostis racemosa*; 33, *Festuca scabra*; 34, *Harpochloa falx*; 35, *Heteropogon contortus*; 36, *Koeleria capensis*; 37, *Microchloa caffra*; 38, *Panicum ecklonii*; 39, *Poa binata*; 40, *Sporobolus africanus*; 41, *Themeda triandra*; 42, *Trachypogon spicatus*; 43, *Tristachya leucothrix*; 44, *Polygala ohlendorfiana*; 45, *Anthospermum herbaceum*; 46, *Kohautia amatymbica*; 47, *Pentanisia angustifolia*; 48, *Diclis rotundifolia*; 49, *Graderia scabra*; 50, *Hermannia depressa*.

treatment effects. Observed differences for some species between burned/grazed and unburned/ungrazed paddocks were stark, contributing to greater variance for stocking rate, hence less likelihood of detection of its effect.

Testing the response of a species to treatment requires that it is adequately represented in at least one level of the treatment. In any community, many species may be naturally uncommon and therefore insufficiently sampled to be statistically analyzed.

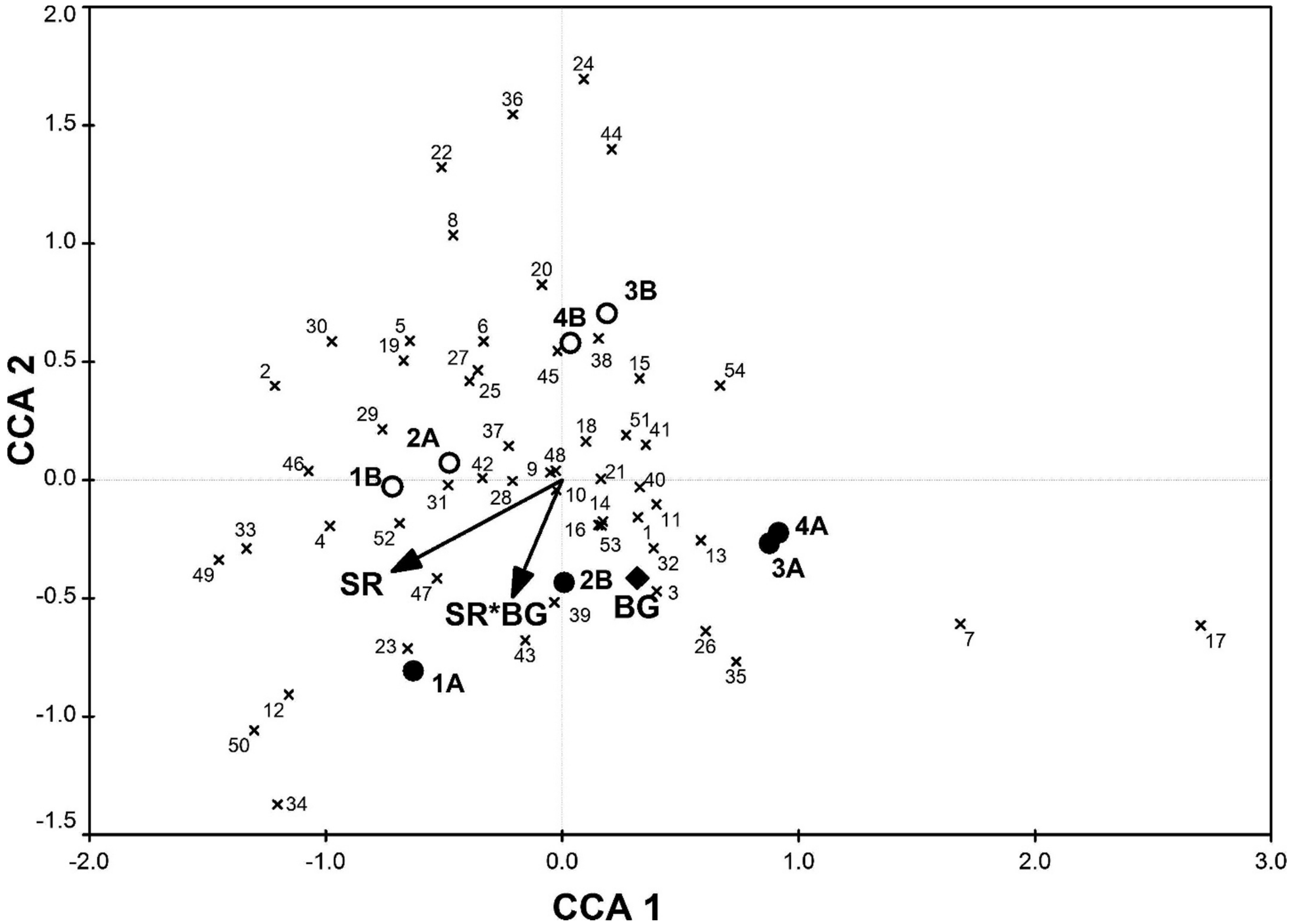

Figure 4. The first two axes of a canonical correspondence analysis for the two-paddock trial on lowland (see Table 2 for results). Key to variables: BG, burned/grazed (versus unburned/ungrazed); SR, stocking rate. Filled symbols indicate paddocks that had been burned/grazed during the season of sampling; open symbols indicate paddocks that had not. Key to species: 1, *Alloteropsis semialata*; 2, *Brachiaria serrata*; 3, *Elionurus muticus*; 4, *Eragrostis curvula*; 5, *Eragrostis plana*; 6, *Eragrostis racemosa*; 7, *Eulalia villosa*; 8, *Helictotrichon turgidulum*; 9, *Heteropogon contortus*; 10, *Koeleria capensis*; 11, *Microchloa caffra*; 12, *Setaria nigrirostris*; 13, *Sporobolus africanus*; 14, *Themeda triandra*; 15, *Trachypogon spicatus*; 16, *Tristachya leucothrix*; 17, *Bulbostylis oritrephes*; 18, *Cyperus sphaerocephalus*; 19, *Albuca setosa*; 20, *Eulophia* sp.; 21, *Hypoxis angustifolia*; 22, *Hypoxis argentea*; 23, *Hypoxis costata*; 24, *Ledebouria cooperi*; 25, *Ledebouria ovatifolia*; 26, *Satyrium* sp.; 27, *Acalypha punctata*; 28, *Acalypha schinzii*; 29, *Ajuga ophrydis*; 30, *Anthospermum herbaceum*; 31, *Anthospermum rigidum*; 32, *Chaetacanthus burchellii*; 33, *Diclis rotundifolia*; 34, *Gerbera ambigua*; 35, *Gnidia kraussiana*; 36, *Graderia scabra*; 37, *Helichrysum adenocarpum*; 38, *Helichrysum aureonitens*; 39, *Helichrysum herbaceum*; 40, *Helichrysum miconiifolium*; 41, *Helichrysum pilosellum*; 42, *Hermannia depressa*; 43, *Hibiscus aethiopicus*; 44, *Kohautia amatymbica*; 45, *Lotononis corymbosa*; 46, *Monsonia grandifolia*; 47, *Pentanisia angustifolia*; 48, *Polygala ohlendorfiana*; 49, *Rhynchosia totta*; 50, *Scabiosa columbaria*; 51, *Sebaea sedoides*; 52, *Senecio bupleuroides*; 53, *Senecio retrorsus*; 54, *Vernonia natalensis*.

This was compounded in this study for grazing-sensitive species. First, these experiments were sampled after more than a decade after implementation of grazing treatment. Second, the experimental sites had experienced a history of heavy grazing prior to trial establishment. The property was used as grazing commonage for the town of Kokstad for nearly a century prior to the establishment of an agricultural research station in 1962, after which they experienced repeated grazing (Peard 1980). The significance of such a history of grazing is that the flora of Highland Sourveld vegetation evolved under light wildlife stocking densities, such that conservative livestock stocking rates are estimated to be 35 times higher (Rowe-Rowe and Scotcher 1986). It is therefore a plausible postulation that many grazing-sensitive species had been markedly reduced, or even extirpated, on these sites by the time of this study. Apparent support for this postulation was the poor representation of growth forms considered vulnerable to grazing, such as large fleshy plants and trailing climbers in the grass canopy (O'Connor 2005). Results of this study are therefore more likely to reflect the response of relatively common, less grazing-sensitive species to grazing treatment. This caveat possibly applies to grazing trials worldwide. This dilemma can only be obviated by targeted monitoring of uncommon species from the inception of a trial.

Effect of Livestock Grazing on Plant Diversity

Notwithstanding the limitations of field experiments, these trials clearly revealed that stocking rate and cattle-to-sheep ratio had an effect on the occurrence of plant species. A total of 22 of 157 species tested showed a response to one or both of these variables, comprising eight grass, two sedge, one no-graminoid monocotyledon, and 11 herbaceous dicotyledon species. The response of grasses is well known and accorded with the increaser–decreaser classification used for rangeland management in South Africa (Tainton 1999). An increase in the mtshiki group of grasses comprising *E. curvula*, *E. plana*, and *Sporobolus africanus* is symptomatic of deterioration in grassland composition in this vegetation type (Hurt and Hardy 1989; Short et al. 2003). Response of grasses to treatments is described in detail in Short (2010). The increaser–decreaser classification applied also to sedges and forbs in relation to stocking rate, which has not been previously described for South African grassland. Sedges had one representative of either response, whereas there were five forb species that behaved as increasers, two that behaved as decreasers, and one species that was most abundant at intermediate levels. In addition, *P. angustifolia* responded as a decreaser in the two sheep stocking rate trials but as an increaser in the simulation trial. A study of grazing gradients across the landscape ranging from heavily impacted through to relatively pristine environments has identified a far greater number of nongraminoids that behave as increaser or decreaser species (Scott-Shaw and Morris, unpublished data). In terms of the effect of cattle-to-sheep ratio, there were only examples of decreaser species in relation to an increasing proportion of sheep.

An increaser–decreaser dichotomy for nongrass plant species in response to livestock grazing has been shown across a wide range of environmental conditions (Noy-Meir et al. 1989; Stohlgren et al. 1999; Vesk and Westoby 2001; Landsberg et al. 2002; McIntyre et al. 2003). However, a fair proportion of species do not respond consistently over a broad geographic (environmental) range (approximately 25% for Australia—Vesk and Westoby 2001).

Whether a higher stocking rate would have a negative or positive effect on species abundance would depend on the palatability and life history attributes of a species, as well as on the pattern of utilization by a specific herbivore species. Cattle do not generally select strongly for forbs (Owen-Smith 1999), although their trampling impact on account of their body size may be inimical to certain growth forms (Witkowski et al. 2001; O'Connor 2005; Uys 2006). By contrast, forbs may form 30–60% of a sheep's diet (Owen-Smith 1999). Palatable forbs with certain attributes might be vulnerable to local extirpation under sustained livestock grazing. For species that are long-lived, have low reproductive output, and recruit infrequently and in small numbers, sustained grazing could result in local extirpation through a combination of increased adult mortality owing to severe defoliation, increased seedling mortality owing to defoliation and trampling, continued livestock consumption of reproductive output, and subsequent decline of the seed bank and of seedling recruitment (see O'Connor 1991). Dicotyledonous forbs should be more vulnerable than grasses to defoliation because their meristematic regions are well above ground. Unfortunately, it was not possible to profile the vulnerability of forb species to grazing impact because of a dearth of study of their life histories in South African grasslands. The only documented example of a livestock-induced decline of a grassland forb is in fact of a monocotyledon geophyte (*Kniphofia umbrina*), a species whose growing point is relatively protected (Witkowski et al. 2001).

Responses are in general agreement with the sparse international literature addressing livestock impacts on plant diversity.

Species vs. Indices

If research is to contribute toward formulating management recommendations for mainstreaming of plant diversity conservation into livestock grazing systems, then rangeland ecologists need to be in accord regarding how to represent and measure plant diversity. One approach is to assess plant diversity in terms of diversity indices (McNaughton 1983; Collins and Barber 1985; Collins et al. 1998; Olff and Ritchie 1998; Stohlgren et al. 1999; Hickman et al. 2004). Calculated indices, such as H' or J' used in this study, may demonstrate that the organization of communities differs, but they cannot identify whether species have been lost through grazing. These indices were of limited value in this study. Although an increase in species richness in response to grazing is usually interpreted as a positive response (provided they are not exotic species), such increases in the studies cited above were mainly due to an increase in the number of annual forb species. This would disguise any decline of perennial forb species that are vulnerable to grazing. There is little evidence that annual species require management for ensuring their persistence as their life history strategies ensure this. Rather, management needs to be directed toward species that could trend toward extirpation, for which appropriate functional groups need to be identified (McIntyre and Lavorel 2001; Diaz et al. 2007). We suggest that emphasis needs to be placed on observing the response of functional groups that are considered most vulnerable to grazing, if realistic insight is to be gained about the potential for mainstreaming conservation of plant diversity into livestock production.

IMPLICATIONS

Cattle-to-sheep ratio and stocking rate affect forb species richness in South African grasslands, and would presumably have similar effects in grasslands of similar structure elsewhere. These effects present a challenge for mainstreaming of plant conservation into livestock ranching. Conservation would favor less use of sheep (except on hill slopes, because heavy-bodied animals induce erosion more readily) and lower stocking rates, but this may be in conflict with producer objectives. Stocking rates that can maintain a productive grass sward of sound composition for livestock production would thus seem too high for maintaining forb richness, owing to differences in livestock impact on these two growth forms.

Insights about the influence of livestock grazing management can be gained from formal grazing trials even if baseline measures are not obtained, but complementary approaches are needed if a sufficient body of knowledge for making recommendations is to be collected in a short period of time. Other study approaches could include fence-line contrasts of two properties practicing different grazing systems (Noy-Meir 1995); gradient studies for identifying which species respond to sustained heavy grazing (McIntyre et al. 2003), and increased study of which species are directly impacted by grazing or trampling. Increasing this knowledge base is essential if commercial rangelands are to realize their potential for maintaining conservation of South Africa's grasslands.

ACKNOWLEDGMENTS

We thank the many staff of the KwaZulu-Natal Department of Agriculture who maintained these experiments over the years. Some financial assistance for G. Martindale was received from the National Research Foundation of South Africa (NRF2069152).

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