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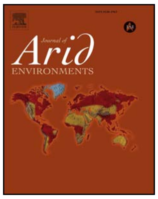

Impact of sheep grazing intensity on vegetation at the Arid Karoo Stocking Rate Trial after 27 years, Carnarvon, South Africa

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ABSTRACT

Sustained heavy grazing is expected to result in degradation and loss of biodiversity in drylands but long-term experiments which assess the impact of management practises on biodiversity are necessary. The effects of stocking rate (SR) on vegetation composition, abundance of different plant functional groups (PFGs), abundance of dominant species, and plant diversity were investigated after 27 years at a long-term SR trial. Vegetation composition was investigated using Canonical Correspondence Analysis and General Linear Models. Stocking rate and time had significant effects on species composition. Increases over time were apparent for total plant cover, palatable shrub cover, and perennial grass cover, annual grass cover decreased over time, whereas other PFGs and rangeland condition showed no trend over time. Greater stocking rates resulted in lower total plant cover, palatable and unpalatable shrub cover, perennial grasses, and annual herbaceous species. Higher annual rainfall resulted in higher total plant cover, while greater preceding three-month rainfall benefitted annual grasses and annual herbaceous species. Plant diversity seemed unaffected by SR. Vegetation structure did not seem to be influenced by SR after 27 years. Our study confirms the slow rate at which vegetation change occurs in drylands and highlights the importance of long-term monitoring trials.

1. Introduction

Drylands (hyperarid, arid, semi-arid and dry sub-humid zones) cover 47% of the world's surface (Le Houerou, 1996). Within southern Africa, the Nama Karoo Biome is the second largest biome covering an area of 607 235 km^2 (23%) within South Africa, Namibia and Botswana (Rutherford, 1997). This vast area is used almost exclusively as rangeland for livestock production (Dean et al., 1995), a land use that contributes indirectly to biodiversity conservation through maintaining natural vegetation (O'Connor and Kuyler, 2009). Management for livestock production faces the challenge of climatic cycles about 18 years in period (Tyson and Preston-Whyte, 2000), with drought years a common experience (Snyman, 1998) and even years of occasional floods. Variable rainfall supports relatively stable long-lived dwarf shrubs and perennial grasses as well as a more variable short-lived grass and seasonal above-ground ephemeral component consisting of herbaceous annuals and long-lived geophytic species. Annual species are often only successful during years with specific rainfall conditions and may otherwise be absent (Dreber et al., 2011). This host of growth forms each respond to inter-annual rainfall variability in a unique way and collectively determine species richness for the Nama Karoo (Cowling et al., 1994). Despite new threats to the biodiversity of the Nama Karoo including alien invasive species, open-cast mining, and renewable energy installations, rangeland mismanagement remains the most important influence because > 80% of the Nama Karoo is used as commercial farming rangeland.

Heavy grazing is one of the main causes of degradation and loss of biodiversity in arid and semi-arid rangelands (Milton, 1994; Milton and Hoffman, 1994; Haarmeyer et al., 2009). Appropriate grazing practices are necessary to ensure the sustainability of the current land use of this vast region. Management practices that can have a pronounced influence on the vegetation dynamics of semi-arid shrublands include stocking rate, grazing systems (including the season of grazing), and animal type, of which stocking rate is widely considered to be the most important (O'Reagain and Turner, 1992). In order to understand the long-term effects of grazing, long-term studies are necessary on account of the pronounced inter-annual variability of rainfall, hence long-term experiments are of exceptional value.

Grazing behaviour reflects the relationship between the animal and rangeland vegetation upon which animals depend (Kasshun et al.,

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Nomenclature

SANBI (South African National Biodiversity Institute) http://newposa.sanbi.org./ National species list (last updated 6 June 2016); Germishuizen and Meyer, 2003

2008). Thus, rangeland condition is an important consideration for decision making in improving grazing and rangeland management systems under arid and semi-arid conditions (Kasshun et al., 2008). At a paddock scale, injudicious grazing management in the Karoo can alter vegetation composition and soil properties (Du Toit et al., 2011). Expected changes of sustained heavy grazing are a change in plant species composition, changes in dominant species, life-forms and growth forms as well as changes in net primary productivity (Milchunas and Lauenroth, 1993). In addition, unpredictability of the seasonal climate can easily result in the deterioration of vegetation if stocking rates are not managed accordingly (Dreber et al., 2011) with the local extinction of vulnerable plant species more readily expected owing to the combination of droughts and sustained grazing (O'Connor, 1991). Vegetation composition, especially the palatable and unpalatable components thereof, is thus central to decision making in arid and semi-arid environments justifying study of vegetation compositional change. In addition, the positive relationship found between climatic heterogeneity and growth form diversity (Cowling et al., 1994) justifies the study of growth form composition and change.

Maintaining biodiversity is a challenge of global concern (Bélair et al., 2010). This challenge cannot be realistically met through the creation of additional protected areas but it is most likely to be met through mainstreaming of biodiversity conservation within the production sector (Pierce et al., 2002). Livestock ranching is one of the best options available for accomplishing this because it relies primarily on the use of natural vegetation (O'Connor et al., 2011) and the same concerns about the effect of grazing management variables on sustainability of production apply to the maintenance of biodiversity. Earlier work on land degradation in the arid shrublands of South Africa reviewed by Dean et al. (1995) emphasised the links between land degradation and less productive rangeland, but gave little attention to the implications of degradation for biodiversity. However, livestock production, not biodiversity, was the overriding interest in degradation during the period of their review (Rutherford and Powrie, 2010), but a foundation for managing rangelands for maintaining biodiversity is now required as a matter of priority. Vegetation compositional change is expected in response to grazing, with species lost or gained over time, as well as the increased threat of alien species, however, the effects on plant diversity are unknown. Formal field experiments provide an opportunity to gain a relatively precise assessment of the impact of specific management variables. An initial focus on plant diversity is critical because it underpins the trophic structure of a food web.

The slow nature of rangeland degradation makes the observation of vegetation change difficult without prior monitoring (Van Rooyen, 1998) reinforcing the importance of long-term trials. The Arid Karoo Stocking Rate Trial, near Carnarvon, is an example of a long-term grazing trial in the Nama Karoo Biome of South Africa. This experiment was initiated in 1988 in order to investigate the influence of stocking rate (number of animals allocated to an area of land) on the Nama Karoo vegetation. The range of stocking rate treatments and length of study period (27 years) offers an opportunity to examine the effect of stocking rate over a longer period than that of a climatic cycle.

The aim of the study was to investigate the effect of stocking rate on vegetation composition, abundance of different PFGs, abundance of dominant species, and plant diversity. The following key questions were investigated: (1) What is the effect of stocking rate on vegetation composition? (2) Does, as expected, an increase in stocking rate depress total plant cover? (3) Does an increase in stocking rate result in a decrease of palatable perennial species and an increase of unpalatable perennial and of annual species? (4) Are annual species successful only under a restricted range of seasonal rainfall, and is their success further dependent on stocking rate? (5) Is the response of the five most dominant perennial species the same as the response of their respective PFGs? (6) Does stocking rate decrease species richness and diversity?

2. Study area

Carnarvon Experimental Station is situated approximately 20 km west of Carnarvon in the Northern Cape, South Africa, at 30°58′S and 21°58′E at an altitude of about 1300 m above sea level. This area is considered representative of the north-western Karoo which has been used for mainly sheep farming for more than a century (Meyer, 1992). Mean annual temperature is 15.2 °C (Mucina et al., 2006) and mean annual rainfall 215 mm, with rain falling mostly in autumn (March) in the form of thunderstorms. Inter-annual variation is high (CV 39.4%). The period from 1931 to 1971 was drier (average 195.8 mm p/a) than after 1972 (average 245.0 mm p/a), with a trend of an increasing concentration of rainfall during the summer months. There was evidence of a cycle with an approximate 22-year period (Du Toit et al., 2015).

The trial is located in the Western Upper Karoo (NKu1) vegetation type (Mucina et al., 2006). Vegetation is dominated by the shrub species *Lycium cinereum* and the dwarf shrub species *Chrysocoma ciliata, Eriocephalus ericoides, E. spinescens, Helichrysum luciloides, Osteospermum spinescens, Pentzia spinescens, Pteronia glomerata, Tetragonia arbuscula* and *Ruschia intricata* (Mucina et al., 2006). Grasses common to this vegetation type are *Aristida congesta, Enneapogon desvauxii, Stipagrostis ciliata* and *S. obtusa* (Mucina et al., 2006) but grasses are relatively sparse at the trial site.

The topography of the 324 ha trial area is gentle varying between 1300 and 1320 m above sea level. Most of the experimental station is situated on a shallow soil variant (depth ± 120 mm) of the Mispah soil form, Myhill 1100 family (Meyer, 1992). The Orthic A-horizon has an average clay content of 10–12% and shows a high rate of water absorption. These stable soils have a low erosion potential. Locals consider these soils to be poorly productive (Meyer, 1992). Two small ephemeral water courses, occupying less than 2% of the trial site, traverse the experimental site. These soils belong to the Valsrivier soil form (Helvetia 1221 family) and are slightly deeper with an effective soil depth of 300 mm (Meyer, 1992).

3. Methods

3.1. Grazing trial

The Carnarvon Experimental Station was purchased in 1962 and since 1963 has been managed at moderate stocking rates based on the concept of maximum profit in the short-term while still maintaining rangeland condition in the long-term (Van den Berg and Du Toit, 2014). Four stocking rate treatments (expressed in terms of hectares per small stock unit (SSU)) were investigated at the trial site. Stocking rate treatments, established in 1988, were 4 ha/SSU (Very Heavy), 5.5 ha/SSU (Heavy), 7 ha/SSU (Moderate) and 8 ha/SSU (Light), (Van den Berg and Du Toit, 2014). In order to aid understanding in this paper, stocking rate treatments are henceforth expressed in an unconventional means as stocking rate per 100 ha i.e. 25 SSU/100ha (Very Heavy), 18 SSU/100ha (Heavy), 14 SSU/100ha (Moderate) and 12.5 SSU/100ha (Light). Paddock sizes were varied in order to obtain the desired stocking rates i.e. Very Heavy, 18 ha; Heavy, 24 ha; Moderate, 30 ha and Light, 36 ha. A total of 12 paddocks (324 ha) were grouped into three blocks of four paddocks each and the four treatments assigned randomly within each of the four blocks (Van den Berg and Du Toit, 2014). Each paddock is 500 m in length and the width varied in order to attain the correct paddock size for each stocking rate. The total trial area was rested for 18 months before the onset of the trial to reduce any pre-existing grazing differences that there may have been (Meyer, 1992). Since 1988, the trial has been managed as a three-paddock system, where livestock are moved every six weeks between two paddocks while the third paddock is rested for a whole year. Dry Afrino ewes were used as trial animals, but were replaced by Dorper ewes in 1996 as this breed was more commonly used by land users at the time (Meyer, 1992). In 2006 the Dorper ewes were again replaced by Afrino ewes when the Dorper flock was donated to emerging farmers.

3.2. Field surveys and derived data

Vegetation composition was sampled using the descending point method (Roux, 1963) in which a rod is lowered at 1 m intervals marked on a rope. One thousand points per paddock were surveyed in two 500 point lines running diagonally through each paddock. When the rod passed through a canopy, the species struck was recorded. Each species is recorded separately as well as the strikes observed on the specific species. Range condition is calculated from these data (see later in Methods). Surveys were conducted at the onset of the trial in 1988 and repeated in 1991, 1998, 1999, 2000, 2001, 2002 and 2015.

Field surveys to assess plant diversity were conducted in May 2015. Ten plots were systematically distributed across each paddock in order to ensure comprehensive coverage, allowing for a 50 m edge effect and avoiding drainage lines. Three plots were placed parallel to and 50 m inward of each 500 m fence, another four plots were distributed parallel to the 500 m fence across the centre of the paddock. Plots outside (10) but adjacent to the trial area, subject to prescribed grazing management, were also surveyed. All the plots were 5 m × 5 m in size with a 1 m × 1 m plot placed in the north-western corner of the 5 m × 5 m plot. Within each 1 m × 1 m plot all the species and number of individuals (density) were noted. In the larger 5 m × 5 m plots, all additional species were recorded. Cover percentage of each species within a 5 m × 5 m plot was visually estimated. In addition, for each live or dead plant intercepted along a line placed diagonally through a plot, measurement was made of its projected aerial cover using the line intercept method (Mueller-Dombois and Ellenberg, 1974) and its height. The distance of the plot from any watering point or resting place was also noted. A comprehensive species list of each paddock was compiled by walking through the paddock until no additional species had been noted for 5 min.

3.3. Data analysis

3.3.1. Overall vegetation composition

Canonical Correspondence Analysis (CCA), a direct gradient analysis technique, was used to describe whether compositional variation over time across treatments was influenced by stocking rate, annual rainfall, and time (year) since inception of the trial, using the CANOCO package version 4.55 (Ter Braak and Smilauer, 2002). Scaling was focused on inter-species distances using biplot scaling, and species data were not transformed. A 'cumulative effect of stocking rate' was examined using the interaction of stocking rate and year. An expected dependence of stocking rate on rainfall was examined using their interaction. Annual or uncommon species (fewer than three occurrences) were excluded in order to reduce noise in the data set. Relative abundance was the measure of abundance used. For each year of data, the mean abundance of each species for each stocking rate treatment was used to result in a data set of 32 observations by 34 species. A Monte Carlo test (999 permutations) was used to test the significance of the first axis and of the ordination overall, after which environmental variables were ranked in importance and tested for significance using the forward selection procedure (Ter Braak and Verdonschot, 1995).

3.3.2. Total cover, plant functional groups, species and range condition

Changes in total cover, cover of plant functional groups, cover of dominant species, and range condition resulting from 27 years of grazing treatment were investigated using General Linear Models (GLMs). Main effects were stocking rate, annual rainfall and years of grazing (time). Grazing impacts can be cumulative hence an interaction between years of grazing and stocking rate treatment was included. An interaction between stocking rate and rainfall was included in order to assess any dependence of grazing impact on the amount of rainfall. It was independently tested whether 'cumulative effect of grazing' was confounded with a directional trend in rainfall. For the annuals the preceding three months rainfall was used, while for the perennials the previous 12 months rainfall was used. PFGs were defined based on life history and expected response to livestock grazing; the six used were annual grasses or herbs, perennial grasses or shrubs, and palatable or unpalatable shrubs. The cover of annual herbaceous species could not be analysed using GLM because residuals could not be normalised by transforming the data. Instead, cover data were transformed into a binomial response for proportional data and analysed using logistic regression. GLMs were undertaken using Statgraphics version 15.2.00 (Statgraphics, 2006).

Change in range condition over time was assessed using the Grazing Index Method (GIM) of Du Toit (2000). This method uses the ecological status of the plant species as determined by their grazing index values (Du Toit, 2000) to determine a range condition score value for a tract of land. Differences among grazing treatments in rangeland condition were examined using a Kruskal-Wallis rank sum test in R and Tukey-Kramer (Nemeyi) test for post-hoc analysis in the PCMR Package (Polhert, 2014) written in R. For each treatment, regressions (linear, semi-log and log-log) were used to investigate changes in rangeland condition across treatments over time.

3.3.3. Plant diversity

The average number of individuals per species per plot were calculated for each of the three treatment replicates indicated that the 5 m × 5 m plots recorded considerably more species in total than the 1 m × 1 m plots and thus this sampling unit was chosen for further analysis, which is in accordance with the findings of Pienaar (2002) for the Nama Karoo.

The average cover per species, species richness, Shannon-Weiner Index and evenness were compared between treatments. Diversity parameters were calculated using Vegan (Oksanen et al., 2015) written for R (R version 3.2.2 (2015-08-14), The R Foundation for Statistical Computing, 2015). These parameters were also calculated for PFGs (annuals, geophytes, facultative perennials and perennials) instead of species and were compared between the applied stocking rates.

Species area curves can provide additional information on treatment differences than a pure measure of species richness (Van der Merwe and Van Rooyen, 2011). These curves were constructed for plots adjacent to one another within a paddock. Each 5 m × 5 m plot was treated as a sampling unit and randomly selected plots were added in sequence until all the plots were accounted for. Type III species area curves (Scheiner, 2003) were constructed using three different functions:

1) an untransformed linear function between species richness (S) and area (A): $S = zA + c$, where z and c are constants for the slope and y-intercept respectively;
2) a power function, typically expressed as the log transformation: $\log S = \log c + z \log A$; and
3) an exponential function, expressed as a semi-log function: $S = z \log A + c$.

Table 1
Summary statistics of the canonical correspondence output.

	Axis 1	Axis 2	Axis 3
Eigenvalues	0.027	0.012	0.006
Species-environment correlation	0.883	0.812	0.760
Cumulative percentage variance			
Species data	13.2	19.3	22.4
Species-environment correlation	53.7	78.5	91.4

Table 2
Test statistics for the environmental variables used in the CCA based on Monte-Carlo permutation tests (999 permutations). Variables are listed in the order they entered the forward selection procedure.

Canonical coefficients	F-ratio	p-value
Stocking rate	3.41	0.001
Time	2.83	0.003
Rain	1.13	0.310
Stocking rate x time	0.70	0.769
Stocking rate x rain	0.42	0.988

Analysis of density and cover percentage data for the plots and paddocks were conducted following tests for normality using the Shapiro and Wilk (1965) statistic. Analysis of Variance using R or a Kruskal-Wallis rank sum test were used depending on data properties. Further post-hoc analysis using Tukey-Kramer (Nemeyii) test were conducted in the PCMR Package (Polhert, 2014) written in R.

4. Results

4.1. Overall vegetation composition

The CCA confirmed that stocking rate and rainfall, time, and the dependence of stocking rate on rainfall had a significant effect on both the first axis (F = 3.95, p = 0.001) and on the overall ordination (F = 1.69, p = 0.003) (Table 1). However, this ordination was weak with only 22% of species variance accounted for. Forward selection included environmental variables in the order of stocking rate, time, rain, stocking rate x time, and stocking rate x rain, but only the first two variables contributed significantly to the model (Table 2). Both first and second axes were constrained by both stocking rate and time (Fig. 1).

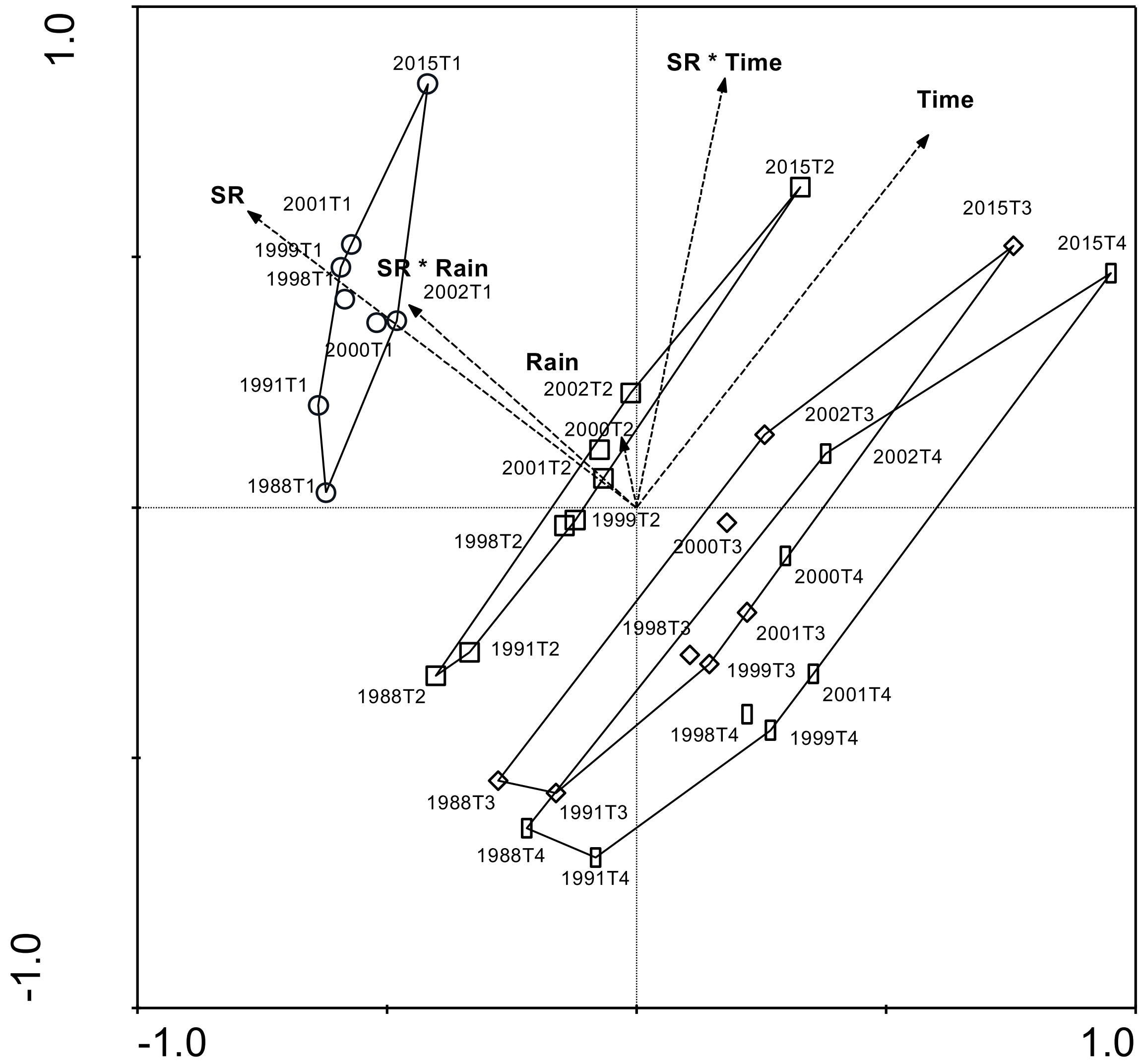

Fig. 1. Results of the Canonical Correspondence Analysis showing samples grouped according to treatment (circles = T1, Very Heavy; squares = T2, Heavy; diamonds = T3, Moderate; rectangles = T4, Light) and environmental variables (arrows). SR = Stocking rate.

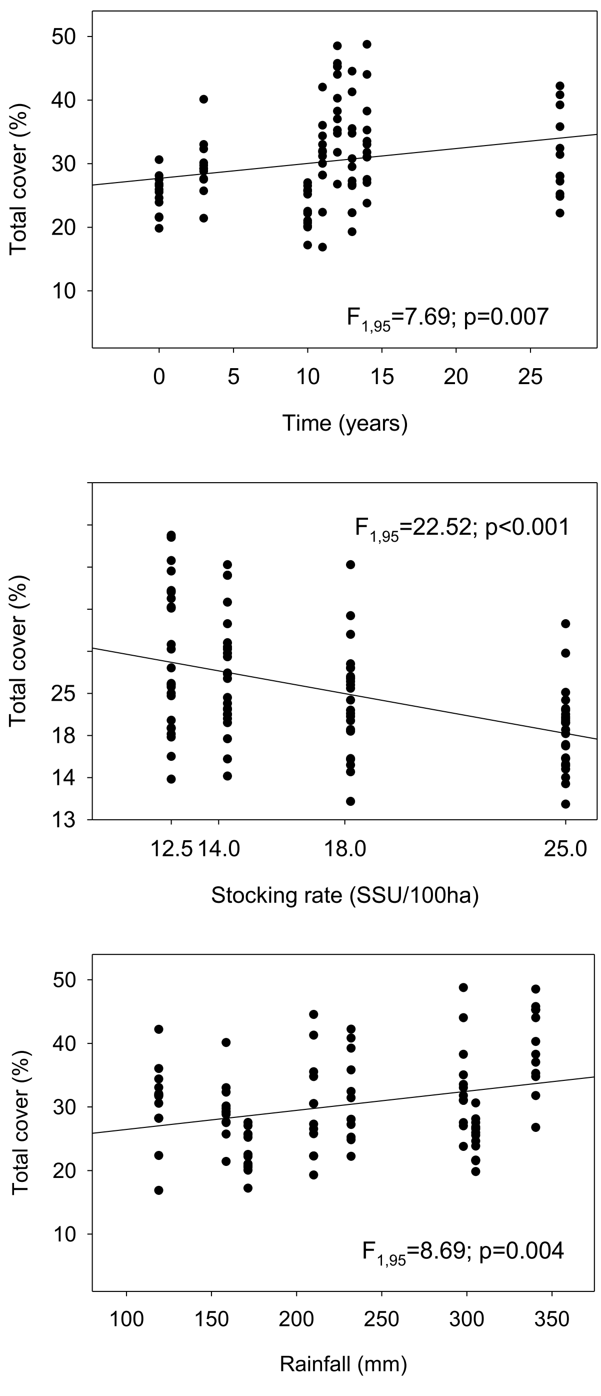

Fig. 2. Relation between total cover and time, stocking rate, and rainfall at Carnarvon. Test statistics derived from GLMs; lines are linear regressions to indicate trend.

4.2. *Total cover, plant functional groups, species and range condition*

4.2.1. *Total cover*

Total plant cover was influenced by time, stocking rate, and rainfall (Fig. 2). There were no significant interactions. Over 27 years cover increased from 25.2 to 31.4%. As expected, cover was inversely related to stocking rate, where it ranged from 34.2% at low to 25.5% at high stocking rates, and to rainfall, where it ranged from 30.6 to 39.4% along a rainfall variation of approximately 120–340 mm per year.

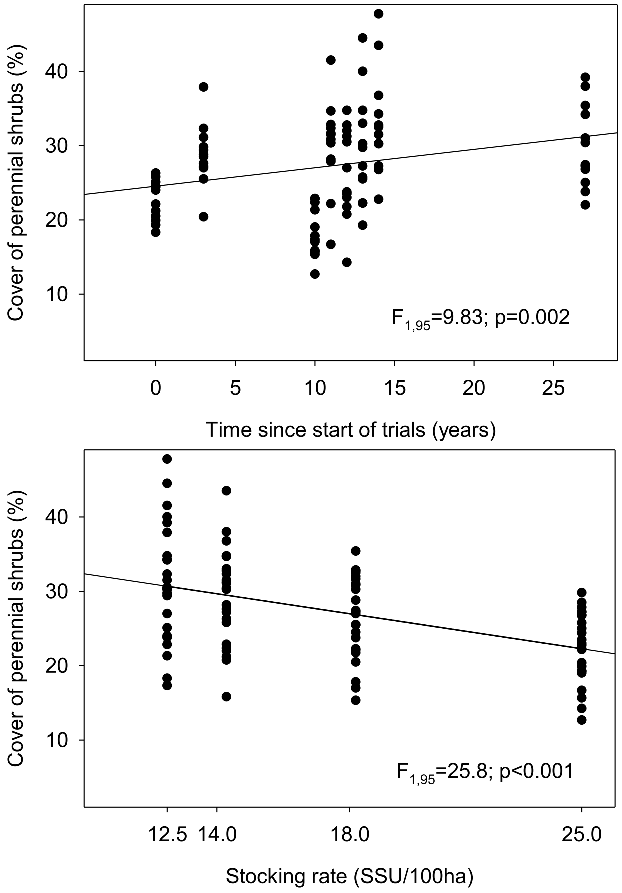

Fig. 3. Relation between cover of perennial shrubs and time and stocking rate at Carnarvon. Test statistics derive from GLMs; lines are linear regressions to indicate trend.

4.2.2. *Cover of plant functional groups*

Cover of perennial shrubs, the dominant growth form, was related to time and to stocking rate (Fig. 3). Cover increased from 22.6 to 30.0% over the duration of the trials, and was lower at high stocking rates (22.5%) than at low stocking rates (31.2%). The palatable and unpalatable components of perennial shrubs responded differently to treatments (Fig. 4). The cover of palatable shrubs was related to stocking rate and time, whereas the cover of unpalatable shrubs was related only to stocking rate. Cover was lower at high stocking rates for both palatable (19.1%) and unpalatable shrubs (3.63%) than at low stocking rates (palatable = 26.3%; unpalatable = 5.6%). The cover of palatable shrubs increased from 18.7 to 26.4% over time, while the cover of unpalatable shrubs was variable but showed no trend over time.

The cover of perennial grass was low (overall average = 0.6%) but nonetheless showed clear responses to treatments. Cover of perennial grasses was strongly related to time ($F_{1,95} = 15.89$; $p = 0.0001$) and to stocking rate ($F_{1,95} = 13.08$; $p = 0.0005$), and there was evidence of a stocking rate × time interaction ($F_{1,95} = 3.19$; $p < 0.078$). Cover of perennial grasses increased in all treatments over time, but the rate at which this occurred was inversely related to stocking rate (Fig. 5). For example, cover increased from 0.20 to 0.40% at high stocking rates, and from 0.10 to 0.83% at low stocking rates.

Annual grass cover was strongly related to preceding three-month rainfall (Fig. 6). In 1999 (year 12) three-month rainfall was 25 mm, and no annual grasses were recorded. In contrast, annual grass cover was 8.5% (the highest ever recorded) the following year in 2000 (year 13)

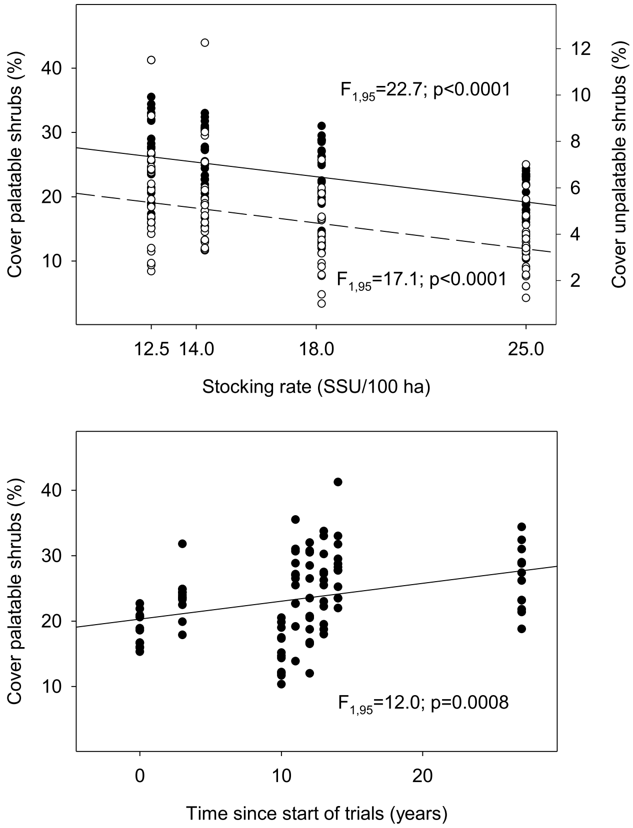

Fig. 4. Relation between cover of palatable (solid markers; solid line) and unpalatable shrubs (open markers and dashed line) and stocking rate (top) and relation between cover of palatable shrubs and time (bottom) at Carnarvon. Test statistics derive from GLMs; lines are linear regressions to indicate trend.

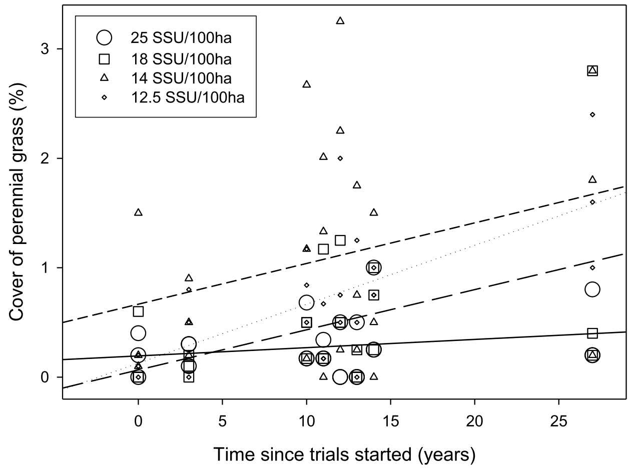

Fig. 5. Relation between time and cover of perennial grasses at four stocking rates at Carnarvon. Test statistics derive from GLMs; lines are linear regressions to indicate trend.

when three-month rainfall was 192 mm.

For annual herbaceous species, a logistic model was highly significant (deviance$_{5,95}$ = 49.76; p < 0.001) and showed a significant interaction between stocking rate and rainfall (χ^2 = 7.91; p = 0.005) (Fig. 7). Time was not a significant term. The positive response of the cover of herbaceous annuals to rainfall was modified by stocking rate in

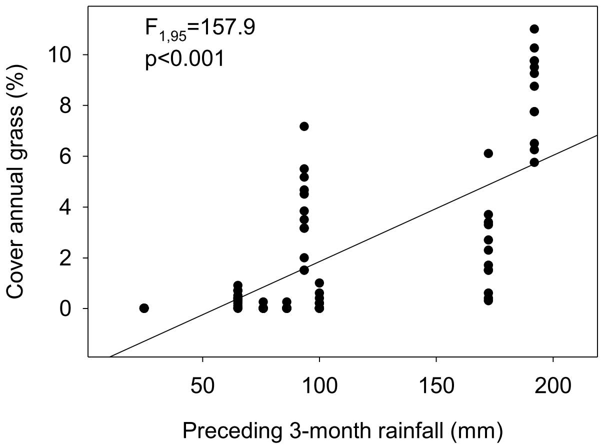

Fig. 6. Relation between cover of annual grasses and preceding three-month. Test statistics derive from GLMs; lines are linear regressions to indicate trend.

that at low stocking rates (12.5 SSU/100ha and 14 SSU/100ha) annual herbs were present only at high rainfall, whereas at high stocking rates (18 SSU/100ha and 25 SSU/100ha) annual herbs were also sometimes present (albeit at low levels) at low rainfall.

4.2.3. *Cover of individual species*

The five most dominant species responded to the stocking rate treatments (Fig. 8). The cover of four of the species (*Pentzia spinescens, Rosenia humilis, Ruschia intricata* and *Eriocephalus ericiodes*) decreased with an increase in stocking rate with one species (*Eriocephalus spinescens*) showing the opposite trend (Fig. 8). Cover of the most abundant species, the palatable *P. spinescens*, increased over time whereas cover of the second most abundant species, the palatable *E. spinescens*, was related to rainfall.

Rangeland condition differed across treatments (χ^2 = 10.622, df = 3, p = 0.014) with a post-hoc analysis indicating significantly poorer condition on Treatment 1 (Very Heavy) than on Treatments 3 (Moderate, p = 0.055), and 4 (Light, p = 0.015). A linear or curvilinear regression indicated no directional trend in range condition on any treatment over 27 years (p = 0.214).

4.3. *Plant diversity*

Stocking rate treatments had no effect on average cover across all species (p = 0.189), species richness (p = 0.816), Shannon-Weiner Index (p = 0.837) or evenness (p = 0.837) recorded in 2015. The number of species per PFG per treatment (annuals p = 0.860, geophytes p = 0.224, facultative perennials p = 0.380, perennials p = 0.130) also indicated that there were no differences between treatments. Our results show that stocking rate treatments have not meaningfully affected plant diversity values after 27 years.

Species area curves fitted for Very Heavy, Heavy and general Farm treatments were best using an exponential function, a power function provided the best fit for the Moderate and Light treatments, whereas an untransformed linear function performed poorly (Table 3). The fact that curves of a different type have been fitted to different treatments suggests that stocking rate has influenced the nature of the curve otherwise it would be reasonable to assume one curve type should have consistently performed better than the other two in this relatively small area. The species area curves begin to asymptote at different plot sizes, at approximately 50 m^2 for Very Heavy, 55 m^2 for Heavy, 70 m^2 for Moderate, 60 m^2 for Light and 45 m^2 for Farm treatments, which indicates an overall uniformity of the vegetation.

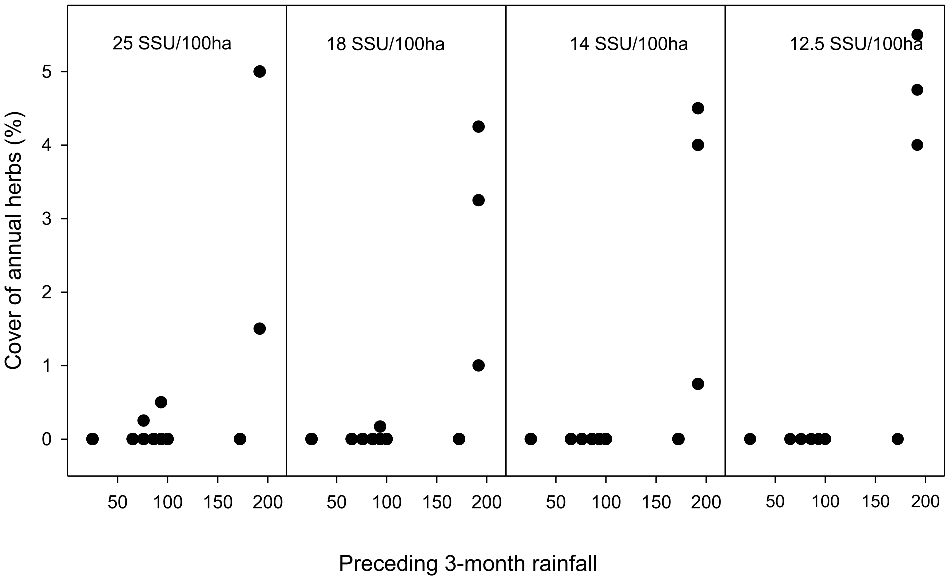

Fig. 7. Cover of annual herbs at four stocking rates at Carnarvon.

Line intercept data indicated no differences between the four stocking rate treatments for average live canopy intercept (average = 2.016, $\chi^2 = 1.582$, df = 4, p = 0.8119) or average live plant height (average = 0.228, $\chi^2 = 2.766$, df = 4, p = 0.5977). Similarly, no significant differences were found for average total canopy intercept (average = 1.796, $\chi^2 = 2.330$, df = 4, p = 0.6754) or average dead plant height (average = 0.159, $\chi^2 = 4.791$, df = 4, p = 0.3094).

5. Discussion

5.1. *Influence of sustained heavy grazing on community structure*

Degradation and the resulting decline in productivity of rangelands across the Karoo have been attributed directly to overgrazing (Acocks, 1953; Milton, 1994; Milton and Hoffman, 1994; Haarmeyer et al., 2009). This appears consistent with a global trend in which grazing has been identified as a factor in the conversion of grasslands to less desirable shrublands, and that shrublands may be inadvertently more intensively grazed than grasslands (Milchunas and Lauenroth, 1993). The expected influence of sustained heavy grazing on compositional change is a loss or decrease in palatable perennial species, an increase in unpalatable perennial species, and an increase in short-lived (annual) components at the expense of perennials (Milchunas and Lauenroth, 1993). However, grazing effects may not be simply predicted in an environment with high inter-annual rainfall variability (O'Connor and Roux, 1995). Instead, a separate account of grazing and rainfall effects, as well as their interactive effect, is required. In corroboration of this need in this study, although a number of expected responses to increased stocking rate were observed such as a decrease in palatable and unpalatable perennial species, there was also an increase in perennial grass cover across all treatments consistent with rainfall effects.

Rainfall is one of the most important drivers of an arid system. Two important rainfall trends over the trial period were increasing annual rainfall and an increasing amount of summer rainfall, with an associated lack of severe drought (Du Toit et al., 2015). A trend of increasing annual rainfall and lack of drought should favour all perennial plants. Accordingly, as shown by the model term 'time', an increase in perennial shrub and grass cover was recorded, even of the palatable shrub, *Pentzia spinescens*, plus an increase in total cover. An increase in summer rainfall is expected to benefit plants with a C4 photosynthetic pathway, that is, both perennial and annual grasses (Roux and Vorster, 1983; O'Connor and Roux, 1995), as was recorded (Figs. 5 and 6). Similar increases in grass cover concomitant with the trial period have been recorded elsewhere in the Nama Karoo (Hoffman and Cowling, 1990; Palmer et al., 1990), this study supporting their conclusion that inter-annual fluctuations in grass and shrub cover had to be accommodated in managing Karoo environments.

We suggest a trend of increasing rainfall may also have masked effects of stocking rate, as the extent of compositional change was not as conspicuous as expected. Even sustained heavy grazing only altered rather than transformed vegetation. In light of drought effects on Nama Karoo vegetation recorded elsewhere (O'Connor and Roux, 1995), we suggest that if this experiment had been initiated between 1940 and 1970, a period in which there was a steep decline in annual rainfall (Du Toit et al., 2015), the outcome would probably have been different.

Compositional change was gradual across all four stocking rates over 27 years. In a global analysis of the effects of grazing (Milchunas and Lauenroth, 1993), it was found that compositional change was slow or absent in many studies. The proposed reason for this minimal change was that in most studies analysed species composition was evaluated many years after grazing treatments had been initiated such that most compositional change had probably occurred long before the sampling period. The fact that our larger trial landscape has been grazed by livestock for at least a century probably plays a role in the limited effect on vegetation of stocking rate measured over the relatively short period of only 27 years. Another cause of the slow nature of compositional change could be short-term annual weather fluctuations and long-term climatic cycles that may override or mask the effect of grazing.

Site-specific grazing impacts on rangelands in the long-term can determine the development of local species pools dominated by PFGs adapted to low or high grazing pressure (Dreber et al., 2011). During vegetation recovery following heavy grazing, both PFGs and species have shown individual responses (Zhou et al., 2011). As predicted, palatable and unpalatable perennial shrubs were found to show a decrease in cover under higher stocking rates. The expectation that annual grasses and herbaceous species should irrupt in good rainfall years (Dean and Milton, 1999; Dreber et al., 2011; Van Rooyen et al., 2015) and should increase with an increase in stocking rate was supported by our results, which indicated annual species reacted to the preceding

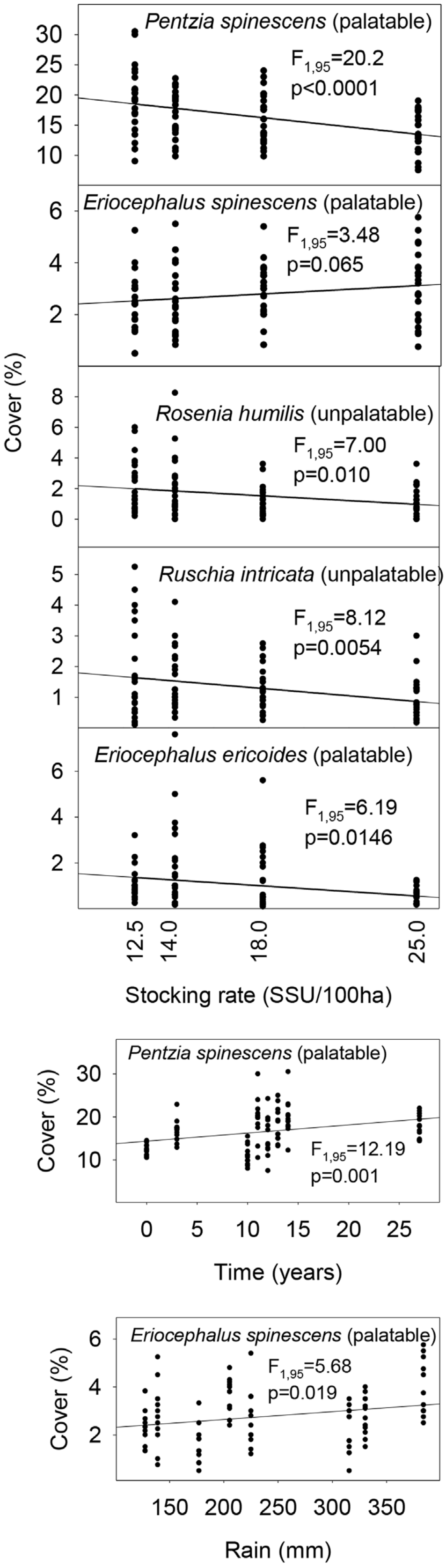

Fig. 8. (both of the above). Relation between cover and stocking rate, time, and rainfall for the five most abundant species at Carnarvon. Test statistics derive from GLMs; lines are linear regressions to indicate trend.

three-month rainfall, although the extent of increase was inversely related to stocking rate. At low stocking rates annual herbaceous species were present only in high rainfall years, but at high stocking rates annual herbs were sometimes present at low rainfall. These results are similar to numerous findings for the closely situated Succulent Karoo Biome vegetation in which heavy grazing has been associated with changes in species and life form composition (Anderson and Hoffman, 2007; Todd and Hoffman, 1999, 2009; Rutherford and Powrie, 2010; Van Rooyen et al., 2015). Hanke et al. (2014) found that changes related to rangeland degradation could be better detected and described at the level of functional groups than at the level of species. Their study found a lack of significant responses in species diversity at sites however, PFG diversity decreased with heavier grazing consistently across ecosystems and scales.

At a plot scale (surveyed only in 2015), no treatment effect was found for average live or total canopy cover, or for average live or dead plant height after 27 years. It therefore appears that these structural parameters had not yet been influenced by stocking rate. However, the descending point method (surveyed eight times since inception of the trial) showed that total cover responded marginally to stocking rate, current season's rainfall, and long-term trend of rainfall (‘time’) The fact that vegetation structure differed only slightly between grazing treatments was attributed to the nature of growth of the dominant growth form, namely dwarf shrubs, of the trial site and surrounding region.

5.2. Maintaining Karoo plant diversity under sustained grazing

Plant diversity, measured by species richness, Shannon-Weiner Index and evenness, seemed unaffected by stocking rate. This was unexpected after 27 years of experimental manipulation. It could be because of the fact that Nama Karoo vegetation is rather species poor (mean = 47, range = 22–76) in comparison to other biomes such as the Succulent Karoo (mean = 74, range = 32–115) (Dean and Milton, 1999). These low species numbers might influence the likelihood of detecting treatment differences. Also, when grazing levels are not excessive, the landscape position in which grazing occurs may be more important than the number of grazing animals or overall intensity of grazing across an area (Milchunas and Lauenroth, 1993). In addition, the grazing system used in this experiment provided each paddock with a years rest that may have masked vegetation change.

Our results are similar to those of a 20 year study on the effects of cattle grazing in arid grassland of the Australian dune swales, where almost no effects of grazing intensity on species abundance, richness and diversity at either small or large spatial scales were observed (Fensham et al., 2010). These authors suggest that short exposure to managed grazing (20 years) has not been sufficient for the full impact of grazing to be expressed, indicating the resilience of these rangelands to the early impacts of sustained livestock grazing. In semi-arid and arid systems subjected to sustained grazing, annual species may increase to compensate for the loss of perennials (Milchunas and Lauenroth, 1993). Results from this study were consistent, with a decrease in the cover of perennial species and an increase in annual species over time. If the notion of two different species pools is supported, that is, a grazing resistant pool and a less grazing resistant pool, then changes in grazing intensity can cause substantial changes in composition with little change in diversity (Rutherford and Powrie, 2010), which is consistent with our findings of change in palatable species cover but not in diversity parameters.

Livestock numbers in the Karoo have been high throughout most of its history (e.g Acocks, 1953; Hoffman and Cowling, 1990) and the provision of additional water has allowed areas to be grazed year-long. By contrast, the original system when subjected to wildlife would only have experienced heavy use on a brief transient seasonal basis when rainfall allowed movement into the area. A history of over a century of sustained livestock grazing in this part of the Karoo may have already eliminated sensitive species and growth forms in certain areas.

Table 3

Species area curves for the four treatments and general Farm treatment constructed using the Untransformed Linear function, Exponential function and Power function for 5 m × 5 m plots added in sequence for the Arid Karoo Stocking Rate Trials (in all cases $p < 0.0001$).

Treatment	Untransformed Linear function		Exponential (Semi-Log) function		Power (Log-Log) function	
	Linear equation ($y = c + mx$)	r-value	Linear equation ($y = c + mx$)	r-value	Linear equation ($y = c + mx$)	r-value
Very Heavy	38.90 + 0.50x	0.68	−14.14 + 21.28x	0.93	2.40 + 0.46x	0.88
Heavy	33.00 + 0.51x	0.85	−14.52 + 19.92x	0.98	2.44 + 0.43x	0.96
Moderate	35.40 + 0.56x	0.92	−13.71 + 21.11x	0.97	2.64 + 0.40x	0.98
Light	27.29 + 0.60x	0.95	−22.84 + 21.84x	0.96	2.29 + 0.46x	0.995
Farm	9.60 + 1.17x	0.93	−35.82 + 24.92x	0.99	0.87 + 0.87x	0.96

Our study design offered a more robust statement about grazing impact on plant diversity than most because of the range of four grazing intensities and the use of a larger sampling unit (25 m^2). In most studies, the response of species richness to grazing is measured using small quadrats (0.5–2 m^2) (Li et al., 2015), few studies have examined grazing effects on biodiversity at multiple scales. Variations in species diversity may not be easily detected without a sufficiently broad gradient of grazing intensity because of the strong resistance of vegetation to grazing (Li et al., 2015). Thus, study design that combines both scaling effect and grazing intensity is critical for an improved understanding on the impact of grazing on biodiversity (Li et al., 2015).

In our study species area curves were produced using 5 m × 5 m plots as the sampling unit and adding randomly selected plots in sequence until all the plots were accounted for as opposed to the conventional use of nested plots. Exponential and power functions produced the best fits, as was also found for the closely situated Succulent Karoo (Van der Merwe and Van Rooyen, 2011). The species area curves fitted could have additionally been influenced by the patterns of local diversity at the southern boundary of the Nama Karoo which have been shown to be greatly influenced by habitats at a smaller scale. Milton (1990) has also shown that run-on habitats with heterogenous soil moisture conditions have higher local diversity than less heterogenous plains habitats. On a global scale, factors noted as reasons for differences in species area curves include differences in patch or habitat size and structural differences in community organisation resulting from different species abundance distributions (He and Legendre, 2002; Scheiner, 2003; Van der Merwe and Van Rooyen, 2011).

5.3. *Role of long-term research*

Long-term research and monitoring can provide important ecological insight and are crucial for the improved management of ecosystems and natural resources (Lindenmayer et al., 2012). The detection of trends in vegetation cover, composition and diversity is especially challenging in drylands because vegetation change in arid ecosystems is often slow (e.g. Cody, 2000; Lawley et al., 2013) on account of the relative potential longevity of dwarf shrubs. Data must be collected over decades in order to gain an understanding of how vegetation responds to short-term, inter-annual variation in rainfall; long-term cyclic rainfall patterns; episodic rainfall events; and grazing pressure (Lindenmayer and Likens, 2010; Van Rooyen et al., 2015). The Arid Karoo Stocking Rate Trial is one of only a few long-term monitoring trials continuing at agricultural research stations within southern Africa and offers a unique opportunity to examine closely the effect of livestock grazing on the vegetation and plant diversity of the Nama Karoo Biome. There are few examples elsewhere in the world of long-term grazing trials despite the importance of rangelands as a land cover. Continuation of this long-term experiment and the need to increase the temporal resolution of sampling, also to ensure main events (e.g. drought) are sampled, will become increasingly valuable as attempts are made to unravel the impact of climate change on already stressed arid ecosystems. An apparent trend of directional change in rainfall evident at this location (Du Toit et al., 2015) and other locations (Du Toit & O'Connor, 2014) in the Karoo are noteworthy owing to their expected influence of proportional representation of perennial shrubs versus perennial grasses (Roux and Vorster, 1983; O'Connor and Roux, 1995). An improved understanding of global change can therefore be sought in experiments of this nature with baseline data in which a known history of land use at a certain spatial scale may be used to interpret possible directional trends.

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