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A 50 year study shows grass cover has increased in shrublands of semi-arid South Africa

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ABSTRACT

In many parts of the world the boundaries between grassland and shrubland biomes have changed substantially over the course of the last century. Many are projected to shift further from being grass-dominated to shrub-dominated by 2050 under global climate change and land use change projections. This paper used long-term surveys and repeat photography to assess vegetation change at the shrubland-grassland ecotone in semi-arid, South Africa. Changes in several climate variables as well as in the cover of grasses and dwarf shrubs over three time periods (1962, 1989 and 2009) were investigated at eight localities within a broad 500 km ecotone between the Grassland and Nama-karoo biomes. Results showed that for most sites grass cover has increased and that dwarf shrub cover has decreased over time. This contradicts earlier views which warned against the expansion of dwarf shrublands in response to over-grazing as well as more recent views which suggest that more mesic biomes in the Karoo Midlands will contract in response to climate-induced aridification. The decline in stocking densities and more conservation-friendly land management practices together with an increase in large wet events in the Nama-karoo biome may have contributed to the increase in grass cover.

1. Introduction

Biome boundaries are recognized globally as areas where changes in the distribution of core terrestrial biomes are likely to first become apparent (Churkina and Svirezhev, 1995; Hufkens et al., 2009). Boundaries between grassland and shrubland biomes have already shifted in many parts of the world (Buffington and Herbel, 1965; Heshmati and Squires, 2011) and are predicted to undergo considerable change in the future (Parton et al., 1995). Most projections suggest that C_4 grasslands will be replaced by C_3 shrublands with shrublands becoming increasingly dominant at the boundary between the two (Leadley et al., 2010). There is further concern that the encroachment of shrubs will impact on community stability and species richness (Alvarez et al., 2012; Báez and Collins, 2008) and reduce biodiversity (Rutherford et al., 2012).

While the reason for the expansion of shrubs is complex, most hypothesized drivers are linked to changes in climate and land use (Archer, 2010; Munson et al., 2012; Okin et al., 2009; Peters, 2002; Peters et al., 2011, 2006; Rutherford et al., 2012; Sala et al., 2000; van Auken, 2009). Climatic factors include increases in temperature and drought frequency, decreasing wind and the effects of increasing CO_2 concentration on plant water use (Archer et al., 1995; Bond and Midgley, 2012; Higgins and Scheiter, 2012; Masubelele et al., 2013; Midgley et al., 2008, 2002; Munson et al., 2011a,b; Parton et al., 1995; Peters et al., 2011). Because frost is limiting for many shrubs, an increase in minimum temperature and a reduction in the frequency of frost under future climate change scenarios (D'Odorico et al., 2010) will favour their expansion. Shrubs are also able to outcompete grasses during drought periods where they have access to deeper soil water (Letts et al., 2010). The water use efficiency and growth rate of C_3 shrubs are both positively influenced by the higher concentration of CO_2 in the

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atmosphere (Morgan et al., 2007) while for C_4 grasses both negative and positive increases in growth rate at elevated CO_2 have been documented (Leakey et al., 2009; Morgan et al., 2011).

Land use change is expected to greatly modify climate change effects and may overwhelm the impact of climate change in some areas (De Baan et al., 2012; Parton et al., 1995). For example, the effect of CO_2 enrichment on soil carbon in the grasslands of the Great Plains is relatively small compared to the impact of ploughing and nutrient fertilization of crops (Burke et al., 1990). Land use on its own is also able to cause a switch from grass to shrub dominance in many semi-arid grassland environments especially when stocking rates and carrying capacity are exceeded (Acocks, 1953; Peters et al., 2006). Bestelmeyer et al. (2007), for example, suggested that the consumption of grassland seedlings by native herbivores has played a role in promoting shrub dominance.

An increase in shrub cover is generally thought to be symptomatic of desertification especially when caused by a combination of livestock grazing and drought (Gibbens et al., 2005; Schlesinger et al., 1990; Scholes, 2009). These two factors likely contributed to the degradation of habitat and the switch from grassland to shrubland between the 1870s and 1930s not only in South Africa (Acocks, 1953) but in many drylands of the world (Gibbens et al., 2005). In some areas, however, an altered climatic regime that consisted not of increased drought, but of increased winter precipitation is also thought to have been responsible for this switch from grasses to shrubs. Under these conditions, the availability of moisture in the cool season favours the establishment of C_3 woody shrubs over C_4 grasses which are generally more active during the warmer, summer months (Booth et al., 2003).

While the majority of studies suggest that shrublands have expanded over time, there are a few studies of grassland/shrubland boundary dynamics which suggest that grasses can recover and dominate shrublands under conditions of high rainfall and low grazing pressure (Peters, 2002). For example, in an earlier study of the Grassland/Nama-karoo shrubland interface in South Africa, Hoffman and Cowling (1990) used repeat photography and a resurvey of existing vegetation data and showed that grass cover had increased significantly at most sites that were previously dominated by shrubs. However, future climate change projections for this and many other semi-arid grassland environments suggested that they will become drier and therefore shrubbier in response to an increase in temperature and drought frequency (Beaumont et al., 2011; Midgley and Thuiller, 2011; Midgley et al., 2002).

Here we report on a study of changes along a semi-arid shrubland/grassland ecotone over the last half century. Nama-karoo shrublands grade into semi-arid grasslands in the Karoo Midlands region of South Africa. We documented the nature and extent of long-term rainfall and vegetation change along the ecotone. Firstly, changes in rainfall and drought incidence were assessed to determine if there was evidence in the historical record for the predicted drying trend which has been projected by global climate change models (Midgley et al., 2002). Secondly, by building on the data sets of Hoffman and Cowling (1990), the nature and extent of vegetation change within grassland and shrubland communities over the last 20 years was considered in terms of future biome-level projections for the region (Midgley et al., 2008). We wished to determine whether shrublands had expanded at the expense of grasslands as suggested by future biome-level projections or whether the trend of an increase in grass cover, reported 20 years ago by Hoffman and Cowling (1990), still holds. Our analysis also explored the relative influence of land use (particularly stocking rate) and rainfall on shrub/grass dynamics with a view to suggesting which key drivers best explain the changes in vegetation cover and composition along this biome boundary. Finally, we considered the implications of these findings for key policy and land management debates in the region.

2. Study area

The study took place along a 500 km transect in the central interior of South Africa from Richmond in the Nama-karoo biome (a semi-arid shrubland dominated by shrubby members of the Asteraceae) in the south west to Dewetsdorp in the Grassland biome in the north east. Eight sites, which were previously surveyed by Roux (1968) and Hoffman and Cowling (1990) were resurveyed in January 2009. All sites were located on colluvial slopes of wide valleys in the region (Roux, 1968). The location and description of each site is summarized in Table 1.

3. Methods

A combination of approaches including analyses of historical rainfall and land use data, repeat photography and long-term ecological monitoring was used to assess changes in the vegetation along a 500 km transect from the shrub-dominated Nama-karoo biome in the southwest to the Grassland biome in the northeast.

3.1. Rainfall

Long-term change in rainfall at representative sites along the transect was assessed. Data were obtained from the South African Weather Service (www.weathersa.co.za). All the time-series data were visually inspected for discontinuities and missing values. Empty cells were replaced with average values for a specific month. Data sets which appeared unreliable with many missing values and discontinuities, such as Wepener, were replaced with the nearest adjacent site for which reliable data were available (e.g. Hobhouse). Annual rainfall was recorded as the sum of values from October the previous year to September in the current year. In addition, the historical incidence of drought along the transect was assessed for a 24 month time scale using the Standardized Precipitation Index (SPI) (McKee et al., 1993). A detailed explanation of the SPI (see Appendix A.2) is provided in Edwards and McKee (1997), Lloyd-Hughes and Saunders (2002) and World Meteorological Organization (2012). A copy of the programme used to calculate the SPI value may be downloaded from: http://drought.unl.edu/MonitoringTools/DownloadableSPIProgram.aspx. Statistically significant changes in rainfall and drought incidence over time were assessed using a non-parametric Mann Kendall test for trend (Modarres & da Silva, 2007).

3.2. Land use

The number of domestic livestock (cattle, sheep and goats) censused over the period 1911–1996 within magisterial districts (Table 1) along the Nama-karoo shrubland/Grassland biome ecotone was obtained from the Agricultural Census Database of the Department of Agriculture. The total number of cattle, sheep and goats recorded each year in a magisterial district was converted to a Large Stock Unit (LSU) value by using the conversion tables in Meissner et al. (1983). LSU values were summed for a magisterial district and stocking rates were calculated by dividing the LSU value by the total area of each magisterial district. The results for the four magisterial districts in the study area which occurred predominantly in the Nama-karoo shrublands were grouped and compared with the grouped results for the four magisterial districts which occurred predominantly in the Grassland biome.

Table 1
Site features of the eight study sites in the Eastern Karoo. Veld Type is from Acocks (1953) and Vegetation Type is from Mucina and Rutherford (2006).

Locality name	Location	Altitude (m)	Magisterial district	Biome	Veld Type	Vegetation Type
Beestekuil	31°14′56.621 S 24°34′45.762 E	1403	Hanover	Nama-karoo	False Upper Karoo	Eastern Upper Karoo (NKu4)
Middelburg commonage	31°28′56.009 S 24°59′41.022 E	1300	Middelburg	Nama-karoo	False Upper Karoo	Eastern Upper Karoo (NKu4)
Geelsbekfontein	31°23′49.091 S 24°07′01.260 E	1551	Richmond	Nama-karoo	False Upper Karoo	Eastern Upper Karoo (NKu4)
Groenfontein	30°53′41.754 S 25°09′25.422 E	1436	Colesberg	Nama-karoo	False Upper Karoo	Eastern Upper Karoo (NKu4)
Hillside	30°09′28.578 S 25°43′33.576 E	1488	Springfontein	Grassland	False Upper Karoo	Xhariep Karroid Grassland (Gh3)
De Draai	30°13′10.013 S 26°23′05.441 E	1503	Smithfield	Grassland	False Upper Karoo	Aliwal North Dry Grassland (Gh2)
Wepener commonage	29°44′25.78 S 27°01′52.62 E	1454	Wepener	Grassland	Transitional Cymbopogon-Themeda Veld	Ecotone Gh2 & Mesic Highveld Grassland (Gm3)
Dewetsdorp commonage	29°34′25.799 S 26°39′52.620 E	1543	Dewetsdorp	Grassland	Transitional Cymbopogon-Themeda Veld	Central Free State Grassland (Gh6)

3.3. Photography

At each of the study sites, matched photos previously taken by Roux (1968) and Hoffman and Cowling (1990) were re-photographed in January 2009 following the approach outlined in Rohde (1997). At each site, the original photo station and exact camera position was relocated, and GPS co-ordinates and altitude recorded. Repeat photographs for the full time series (1969, 1990 and 2009) were matched and analysed in Photoshop CS4. Visual estimates of grass and shrub cover in the photographs were undertaken using the matched images. The complete series is provided as supplementary material (Appendix B) while the original photographs and repeated images as well as the completed field data sheets have been archived with the Plant Conservation Unit's repeat photograph database kept at the University of Cape Town.

3.4. Vegetation sampling

In addition to repeat photography, a quantitative estimate of species cover was also undertaken in the field. This was done by recording the species found at a point every 1.5 m along a transect using the same approach outlined in Roux (1968) and Hoffman and Cowling (1990). At each site in 2009 a total of about 600 points were recorded within 3 parallel transects of 200 points each. The percentage cover estimate for a species reflects the number of points out of 600 (multiplied by 100) recorded for a species. Following the approach by Hoffman and Cowling (1990) the different species were assigned to one of the following five growth forms and changes in the percentage cover of each growth form over time was determined: forbs, geophytes, grasses, sedges (Cyperaceae/Juncaceae), shrubs. In addition, the Grazing Index Value (GIV) was determined for each sample at each time step. This provides a relative measure of the potential forage availability at a site and is a proxy assessment of rangeland condition. It is based on the individual properties of species at a site and is derived from decades of field observations and grazing trial research carried out at the Grootfontein Agricultural College in Middelburg (Du Toit et al., 1995). Using species-specific information, each species was assigned a forage factor on a scale from zero to ten and then multiplied by the percentage cover of the species at the site. This was then summed for all species at the site to indicate the forage potential or GIV for the site for a specific year (Du Toit, 2010b; Du Toit et al., 1995).

3.5. Data analysis

Vegetation cover data for all three time steps (1969, 1990 and 2009) was analysed in PC Ord 5 (McCune and Mefford, 2006) using Non-Metric Multidimensional Scaling (NMMS). The dominant species were shown and site changes at the different timeframes were also depicted using successional vectors in an ordination graph.

4. Results

4.1. Vegetation change – field transects

4.1.1. Nama-karoo shrubland sites

The change in species richness recorded in transects between 1961/2 and 1989 varied between the four Nama-karoo biome sites

Table 2
Changes in species richness, vegetation and growth form cover and the Grazing Index Value (GIV) at four Nama-karoo shrubland biome sites for the periods 1961/2, 1989 and 2009.

Parameters	Beestekuil			Middelburg			Geelbeksfontein			Groenfontein		
Date	Dec 1962	Jan 1989	Jan 2009	Feb 1962	Jan 1989	Jan 2009	Feb 1962	Jan 1989	Jan 2009	Dec 1961	Jan 1989	Jan 2009
Number of points	1000	800	782	1000	550	578	1000	600	599	1000	1000	960
Total number of species	16	30	11	27	25	24	29	27	17	25	26	16
Canopy spread cover (%)	42	62	49	52	72	60	47	66	63	52	59	39
Growth form canopy spread cover (%)												
Forbs	2	2	0	0.5	3	0.4	1	5	0	3	14	0.3
Geophytes	0	0	0	0.1	0	0	0	0	0	0	0	0
Grasses	8	33	21	35	45	44	10	27	18	17	33	24
Sedges	0	0	0	0	0	0	0.4	0	0	3	0.2	1
Shrubs	32	28	28	17	24	16	36	35	45	29	12	13
Shrub:Grass	3.9	0.9	1.4	0.5	0.6	0.4	3.6	1.3	2.5	1.7	0.4	0.6
GIV	107	259	187	186	275	282	160	251	277	189	202	137

(Table 2). At all sites, however, species richness declined in 2009 to values below those first recorded in 1961/2. Total canopy cover increased between 1961/2 and 1989 but declined in 2009. The cover of forbs, geophytes and sedges was generally low at all sites for the three time periods except at Groenfontein in 1989 when forb cover was relatively high.

Grass cover increased at all Nama-karoo sites between 1961/2 and 1989, declining again in 2009 although all sites had increased grass cover relative to the 1960s census (1.26–2.6 fold higher grass cover). The grass species responsible for the increase include *Eragrostis lehmanniana* and *Aristida diffusa* in 1989 but the former declined while the latter continued to increase through to 2009. An increase in the more palatable grass species such as *Tetrachne dregei*, *Heteropogon contortus* and *Digitaria eriantha* is also prominent in 2009.

At three of the four sites shrub cover declined while at all sites the shrub:grass ratio declined between the start and end of the survey period. Shrub species that declined were *Chrysocoma ciliata*, *Walafrida saxatilis* and *Pterothrix spinescens* while *Eriocephalus ericoides* and *Rosenia humilis* maintained a good cover between 1989 and 2009. At all sites in the Nama-karoo biome the Grazing Index Value (GIV) increased between 1961/2 and 1989 but declining again at three of the four sites in 2009. However, relative to the 1960s, there was a net improvement (1.51–1.75 times 1960s values) in GIV at three of the four sites over the half century.

4.1.2. Grassland biome sites

Three of the four grassland biome sites showed an increase in species richness between 1961/2 and 1989 and all showed a decline in 2009 to values below those recorded in the first survey in 1961/2 (Table 3). Total canopy cover increased at three of the four sites between 1961/2 and 1989 but generally declined again in 2009. The cover of forbs, geophytes and sedges was higher in grassland than in Nama-karoo biome sites but never dominated cover values. Grass cover increased at all grassland biome sites between 1961/2 and 1989 and declined again at three of the four sites in 2009. There was a net increase in grass cover at three of the four sites over the 50 year period. At three of the four sites shrub cover as well as the shrub:grass ratio declined over the course of the survey period. At all grassland biome sites the Grazing Index Value (GIV) increased between 1961/2 and 1989 but declined again in 2009. There was a net increase in GIV over the full 50 year period at three of the four sites (1.29–1.72 times 1960s values).

4.1.3. Trajectories of vegetation change

An NMMS ordination of the sites for the three study periods showed that Nama-karoo biome and Grassland biome sites have remained separate from each other over time (Fig. 1). Based on their distance in ordination space, Grassland biome sites appear more dissimilar in composition from Nama-karoo biome sites in 2009 than they were in 1961/2.

There was no suggestion in the data that individual sites within the two biomes have converged on each other over the course of the study period although Middelburg, which is located in the Nama-karoo biome has moved closer in ordination space to Grassland biome sites over the course of the study. For several sites, the difference in composition appeared more different from the period 1961/2 to 1989 than for the time step from 1989 to 2009.

4.2. Photographic evidence of change

A complete collection of all photographs in the time series for all sites is provided in the supplementary data. Four representative sites, two in the Nama-karoo biome and two in the Grassland biome are shown below to illustrate the major trends in each of the biomes, particularly with regard to changes in the abundance of grasses and shrubs over time.

4.2.1. Middelburg commonage (Nama-karoo shrubland example one)

The set of three repeat photographs shown in Fig. B.2 in Appendix B reflects changes within a wide colluvial valley of the Eastern Upper Karoo (NKu4) (Mucina and Rutherford, 2006) over the periods 1962–1989 and 1989–2009. This west-facing site is located on state land at the edge of the town of Middelburg and has not been grazed over the course of the study period. Photographic evidence and survey data show that between 1962 and 1989 there was a substantial increase in cover of grasses such as *E. lehmanniana*, *Aristida adscensionis* and *T. dregei* which replaced *P. spinescens*, a spiny shrub with low forage potential. Other shrubs, with higher forage potential as determined by their Grazing Index Value, such as *Helichrysum lucilioides* and *Plinthus karooicus*, increased in cover between 1962 and 1989. Grass cover in 2009 appeared little different to that of 1989 although the dominant species had changed to *Aristida diffusa*, *E. lehmanniana* and *T. dregei*. Several new, relatively palatable grass species, such as *H. contortus* and *D. eriantha*, were also present in 2009. Dominant shrubs in 2009 were *P. spinescens*, *E. ericoides*, *H. lucilioides* and *Chrysocoma coma-aurea* which reflect a range of GIV values.

4.2.2. Groenfontein farm near Colesberg (Nama-karoo shrubland example two)

This site was located on a gently sloping pediment below a dolerite ridge with deep, well-drained soils. The major change between 1962 and 1989 was the increased cover of grasses dominated by *E. lehmanniana*, *Tragus koeleroides* and *Eragrostis obtusa*

Table 3
Changes in species richness, vegetation and growth form cover and the Grazing Index Value (GIV) at four Grassland biome sites for the periods 1961/2, 1989 and 2009.

Parameters	Hillside			Smithfield			Wepener			Dewetsdorp		
Date	Feb 1962	Jan 1989	Jan 2009	Feb 1962	Jan 1989	Jan 2009	Feb 1962	Jan 1989	Jan 2009	Feb 1962	Jan 1989	Jan 2009
Number of points	1000	600	587	1000	600	580	1000	600	595	1000	600	395
Total number of species	24	25	21	21	25	13	25	23	17	26	30	17
Canopy spread cover (%)	64	68	50	65	93	57	80	62	83	69	94	87
Growth form canopy spread cover (%)												
Forbs	2	0.4	0	0.4	2	0	0.2	1	0.5	1	2	3
Geophytes	0	0	0.2	0	0	0	1	0	0	0	0	0
Grasses	54	58	35	51	79	54	66	75	79	63	88	83
Sedges	0.2	0	0	1	3	0	0.2	1	1	0	0	0
Shrubs	10	9	14	14	9	3	13	3	3	5	4	2
Shrub:Grass	0.2	0.2	0.4	0.3	0.1	0.05	0.2	0.04	0.03	0.08	0.05	0.02
GIV	352	398	333	273	613	353	340	378	534	412	770	710

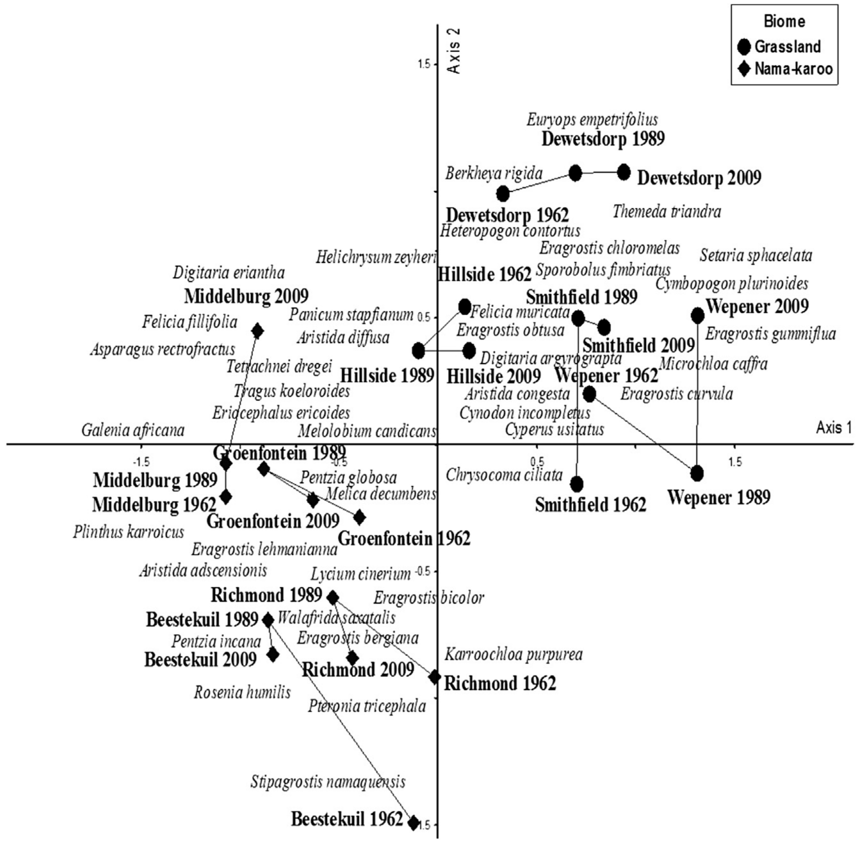

Fig. 1. NMS ordination of the trajectories of change for species in four Nama-karoo shrubland biome and four Grassland biome sites over three time steps (1961/2, 1989 and 2009). The two axes explained 76% of the total variation in the dataset. A two-dimensional solution with a final stress value of 11.4 was selected after 144 iterations ($p = 0.004$).

(Fig. B.4 in Appendix B). The dominant dwarf shrub species in 1989 were *C. ciliata*, *Eriocephalus spinescens*, *Pentzia globosa* and *W. saxatilis* which had all declined substantially in cover in 1989. Grass cover continued to increase in 2009 compared to 1989. The dominant grass in 1989, *E. lehmanniana* had declined in 2009 while *T. koeleroides* and *A. adscensionis* had increased substantially.

4.2.3. De Draai farm near Smithfield (Grassland biome example one)

The site forms part of a wide open plain with low dolerite hills in the background (Fig. B.6 in Appendix B). Termite mounds were common at this site. Photographic and survey data suggest an increase in grass cover at this site and gaps evident in the 1962 photograph were filled by the dominant grasses in 1989 such as *Themeda triandra*, *Eragrostis curvula* and *Cymbopogon plurinodis*. Shrub cover was relatively high in 1962 with *Walafrida saxatilis* and *C. ciliata* dominant. Dwarf shrub cover declined in 1989. The image in 2009 provides some measure of the extent of the drought in the area at the time. Grass cover is generally lower in 2009 when compared to 1989. The dominant grasses in the foreground in 2009 were *C. plurinodis*, *E. curvula* and *T. triandra* which have been heavily grazed. *T. triandra* also declined in cover since 1989. The number of termite mounds also increased in the middle and background sections of the photograph in 2009.

4.2.4. Wepener commonage (Grassland biome example two)

This site forms part of the Wepener town commonage and has been leased as grazing land to several different commercial farmers in the region over the course of the study period (Fig. B.7 in Appendix B). It is located on a gentle north-facing slope at the ecotone between the Dry Highveld Grassland (Gh2) and Mesic Highveld Grassland (Gm3) vegetation types (Mucina and Rutherford, 2006). The cover of shrubs was relatively high in 1962 and was comprised mostly of *C. ciliata*, *Felicia muricata*, and *Helichrysum dregeanum*. By 1989 shrub cover had declined significantly and *C. ciliata* had all but disappeared from the study site. In 2009, the dominant shrub was *F. muricata* and is barely evident in the repeat photograph since the presence of a dominant grass sward has hidden the lower-growing shrub species at the site. Changes in the grass sward are characterized by substantial shifts in the dominance of different species in different survey periods. For example, the dominant grass species in 1962 were *Eragrostis chloromelas* and *Setaria sphacelata* although *C. plurinodis* and *T. triandra* were also present but at lower abundance values. In 1989 *E. curvula* and *T. triandra* dominated the survey site while in 2009 *C. plurinodis* was dominant. Other grass species such as *S. sphacelata*, *E. curvula* and *Microchloa caffra* were also common in 2009 while *E. obtusa* was recorded at the site for the first time.

4.3. Rainfall and drought incidence

4.3.1. Annual rainfall

Long-term annual rainfall did not change significantly (Mann–Kendall test $p > 0.05$) at any of the Grassland biome sites nor at the four Nama-karoo biome sites in the 20th century (Fig. A.1. in Appendix A). The years 1974, 1988 and 2006 reflect periods when annual rainfall was generally higher than normal at most sites while 1933 and 1969 were years of low rainfall at most localities.

4.3.2. Standardized Precipitation Index (SPI)

Trends in SPI values for all rainfall stations in the Nama-karoo shrublands showed a significant increase in wetter conditions over time while there was no change in any of the Grassland biome stations (Fig. 2). The periods between 1976–1978 and 1988–89 stand out at most stations as being years of extremely wet conditions. Severe drought conditions prevailed in the Nama-karoo shrublands in 1928 and 1969 while data from Grassland biome sites were more variable. For Springfontein and Hobhouse the first decade of the 21st century was one of the driest on record.

4.4. Land use

Livestock data between 1911 and 1996 show that stocking rates declined in magisterial districts in both the Nama-karoo shrublands and Grassland biomes (Fig. 3).

5. Discussion

5.1. Change in grass and shrub dominance along ecotones

Ecotones between distinct grass-dominated and shrub-dominated ecosystems occur in many parts of the world in both the northern (Peters, 2002; Schlesinger et al., 1990) and southern hemispheres (Archer, 2010; Hoffman and Cowling, 1990). The majority of such ecotonal studies suggest that shrubs have either expanded or will expand in the future as a result of heavy grazing pressure as well as changes in climate (Gibbens et al., 2005; Midgley et al., 2008; Peters et al., 2006; Schlesinger et al., 1990; Yanoff and Muldavin, 2008; van Auken, 2000). The invasion of cheatgrass (*Bromus tectorum*) in the US (Bradley et al., 2009) and that of *Eragrostis* spp. in many arid lands in the world is well documented (D'Antonio and Vitousek, 1992) but only in a few cases has evidence been presented for an increase in native grass species over time (Cramer et al., 2001; Hoffman and Cowling, 1990; Peters, 2002).

Vegetation changes in the current study show an increase in cover of native grass species and a decline in shrub cover over the period 1962–2009 at most sites. These findings support those of Hoffman and Cowling (1990) who analysed the same sites but over a shorter time period and showed a similar trend in shrub and grass cover. Evidence from our study suggests that the increase in grass cover has been sustained over the last two decades and that Acocks' s(1953) 'expanding karoo' hypothesis is, therefore, not supported by the evidence. Similarly, from the trajectory of change experienced in the region over the period 1962–2009, there is no evidence yet of a contracting grassland biome which has been projected for a warmer South Africa (Ellery et al., 1991; Midgley et al., 2008). Since fire has not occurred at any of the Nama-karoo biome sites over the course of the study period, interpretations of the changes in grass and shrub cover are best explained in terms of the potential role of rainfall, land use, temperature and atmospheric CO_2 concentration.

5.2. Changes in annual rainfall and the incidence of drought

An analysis of the long-term rainfall record suggests no significant trends in annual rainfall totals over the historical period in both the Nama-karoo and Grassland biome sites. This supports the general consensus for southern Africa that there has been no significant change in annual rainfall over the course of the 20th century (Kruger, 2006). Changes in the Standardized Precipitation Index (SPI) over time, however, suggest that localities within the Nama-karoo biome have experienced a significant increase in wet periods (Lloyd-Hughes and Saunders, 2002) while those within Grassland biome sites have remained largely unchanged. Droughts in the region clearly occur at different intensities, spatial extents and durations (Rouault and Richard, 2004) with important implications for the vegetation of the region. Furthermore, Du Toit (2010a) has analysed long-term rainfall data for Middelburg and has shown a significant increase in early season rainfall (Sep–Feb) and a decrease in late season rainfall (Mar–May) at this site. If this trend has been more widespread in the study area then this may be partly responsible for the increase in grass cover observed in the region (O'Connor and Roux, 1995).

5.3. Changes in livestock numbers

The majority of rangelands in our study area are privately-owned and during most of the 20th century have been used primarily for the commercial production of sheep and cattle under extensive ranching conditions (Hoffman et al., 1999). The substantial role of overgrazing in promoting shrub encroachment between the 1800's to the late 1900's is well recognized in many shrubland-grassland ecotones around the world (Peters et al., 2006; Yanoff and Muldavin, 2008). However, evidence from agricultural census records from four magisterial districts in the Nama-karoo biome and four in the Grassland biome show that stocking rates have declined by 45% in the former and by 30% in the latter biome between 1910 and 1996, when the last agricultural census took place. This decline in stocking rate is supported by several other studies in the broader Karoo region (Archer, 2004; Dean and Macdonald, 1994; Dean et al., 1995; Hoffman et al., 1999) although explanations for the decline vary. For example, Dean and Macdonald (1994) ascribe this decline in stocking rate to the loss of primary production and degradation of rangelands as a result of an increase in shrub cover. Hoffman et al. (1999), however, suggest that effective paddock development combined with the widespread practice of rotational grazing have been responsible for the decline in stocking rates.

Changes in the palatability of the species within the rangelands investigated in the current study do not support the view that the decline in stocking rate has occurred because of a decline in forage quality and productivity over time (Dean and Macdonald, 1994). Instead the data point to a consistent increase from 1962 to 2009 in palatable species (Du Toit et al., 1995) such as *A. diffusa*, *C. plurinodis*, *H. contortus*, *T. dregei*, *S. sphacelata*, *T. triandra* and *E. curvula*. In addition, there has been a decrease over the same period in less palatable species such as *Stipagrostis namaquensis*, *P. spinescens*, *E. spinescens*, *Pentzia incana*, *W. saxatilis* and *C. ciliata*. This suggests that rangelands within both the Nama-karoo and Grassland biomes have improved in the amount and quality of forage over time.

Acocks' s(1953) predictions of an expanding karoo shrubland were based on the assumptions that most farmers in the region had overgrazed their land in order to achieve maximum animal production and that karoo shrubs increased with overgrazing. He predicted that if this situation of high stocking rates was to continue unabated, the land would become more degraded with karoo shrubs favoured under heavy grazing impacts. Ironically, however, it was probably Acocks's dire warning of future desertification which raised awareness of the impact of overgrazing and resulted in a reduction in stock numbers in the region. It is now recognized that herbivores can precipitate a switch between the Nama-karoo and Grassland biomes (Rutherford et al., 2012). Continued heavy grazing would have largely been responsible for shrub expansion if it were not for Acocks' s(1953) study which appears to have been crucial in reversing the desertification trend over much of the semi-arid regions of South Africa at the time (Hoffman and Ashwell, 2001).

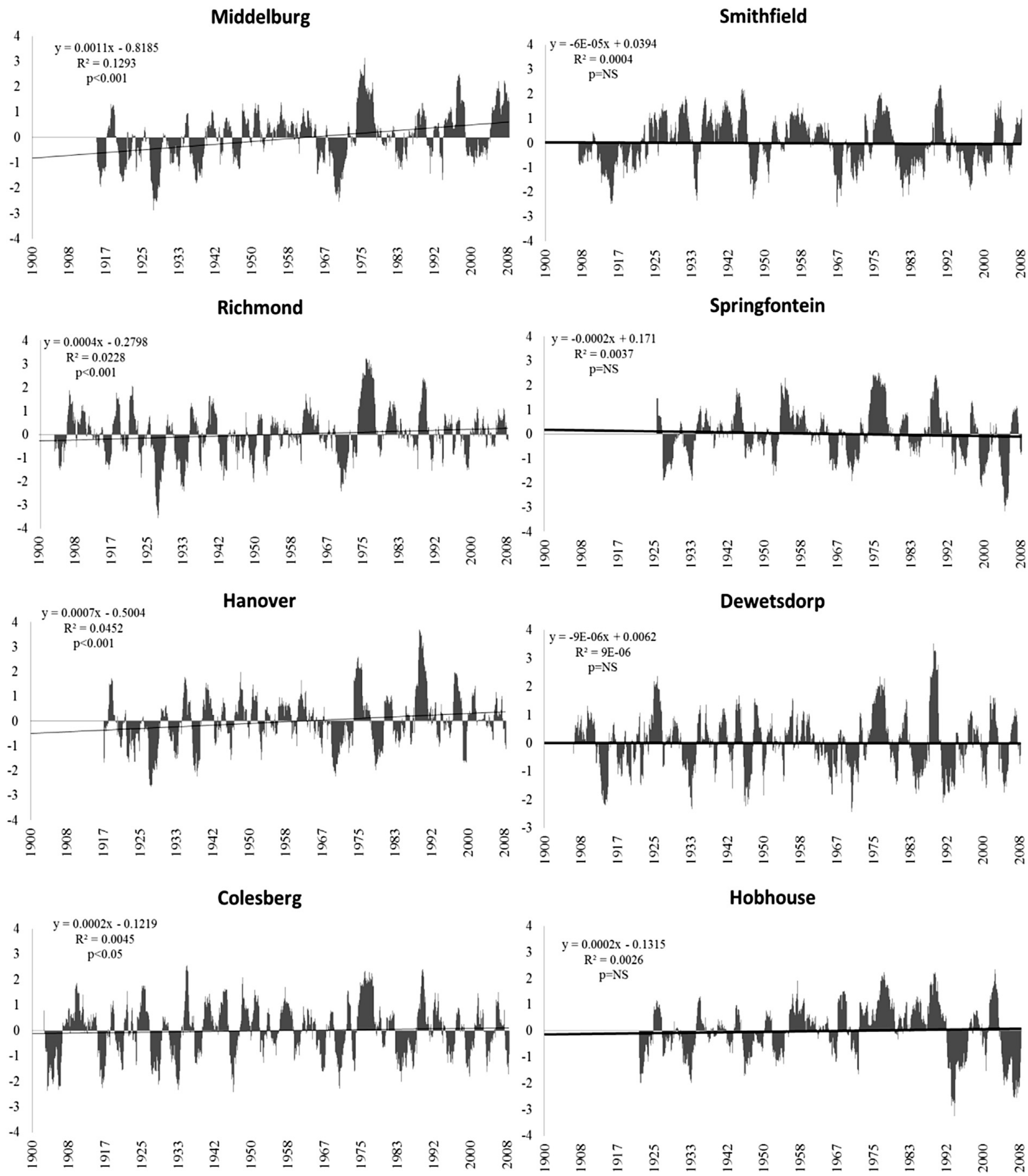

Fig. 2. Standardized Precipitation Index (SPI) values for four Nama-karoo shrubland biome (left) and four Grassland biome rainfall stations (right). The linear trend in the time series and significance of the slope estimate are also shown.

5.4. The dynamics of grasses and shrubs in response to rainfall, grazing and CO_2

Vegetation changes in the current study show an increase in grass cover and slight decline in karoo shrubs. This result can be interpreted in terms of the general models available for the study area. For example, both Hoffman et al. (1990) and O'Connor and Roux (1995) show how seasonal rainfall affects the relative proportions of grasses and shrubs within the ecotone between the Nama-karoo and Grassland biomes. High summer rainfall favours an increase in grass cover while autumn and winter rains are thought to favour shrubs. Furthermore, Milton and Hoffman (1994) present a 'state-and-transition' model for the eastern Karoo in which both grazing and rainfall interact to influence the proportion of grasses and shrubs in an area over years or decades. The results from our study suggest that most of the Nama-karoo biome sites have shown an increase in grass cover while the Grassland biome sites are now dominated by perennial grasses. The improved cover and composition within Nama-karoo biome sites since the 1960s should further result in greater moisture retention and less run-off relative to their shrub-dominated earlier condition. This should enable grasses to continue to dominate if rainfall and stocking rate

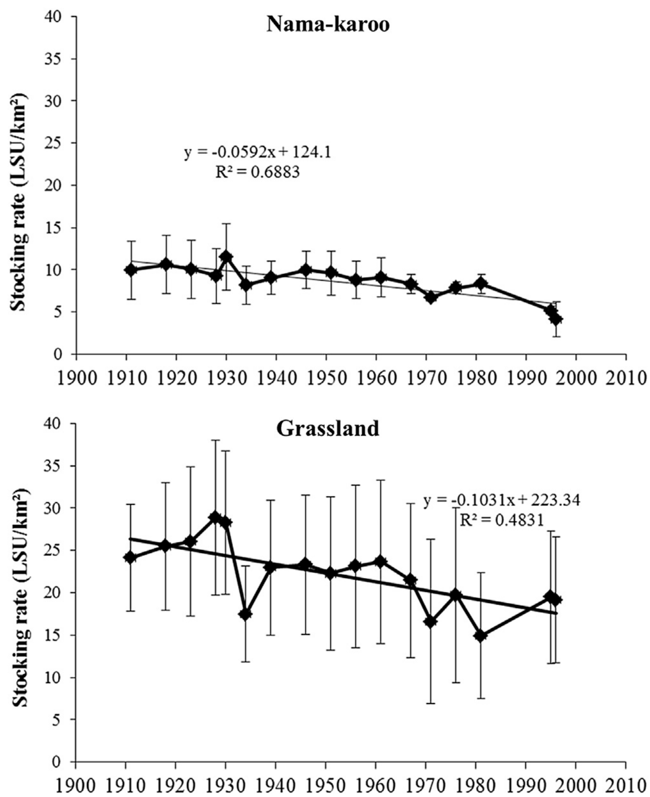

Fig. 3. Change in average stocking rate (Large Stock Unit/km^2) (+SD) within four magisterial districts of the Nama-karoo shrubland biome and four magisterial districts of the Grassland biome.

conditions remain the same. A regional repeat photograph study of the biomes in the Karoo Midlands suggested that the increase in grasses and decline in dwarf shrubs is widespread in the region (Masubelele, 2012). Although fire has not been an important influence on the cover and composition of Nama-karoo shrublands in the past, if grasses were to continue to increase in cover then fires would occur more frequently. If this were to happen then grasses are likely to become even more dominant in the landscape than they are at present.

The increase of grasses in the region is, however, also predicted by dynamic global vegetation models which incorporate the effects of increasing atmospheric CO_2 on grasses and shrubs (Higgins and Scheiter, 2012). Recent FACE experiments in the USA mixed prairie (Morgan et al., 2011) and output from an adaptive Dynamic Global Vegetation Model (aDGVM) (Higgins and Scheiter, 2012) suggest that C_4 grasses might benefit more from temperature and CO_2 increase than previously expected. An increase in soil moisture content is among the most general results of CO_2 enrichment experiments in grasslands and arid shrublands (Morgan et al., 2011). The results of the survey presented here are consistent with the idea that an increase in temperature and CO_2 might benefit grasses. Although long-term temperature data are available for only a few sites in the eastern Karoo, the trends are for an increase in both maximum and minimum temperature over the last 40 years. Unravelling the effects of changes in rainfall seasonality, land use, temperature and CO_2 enrichment, are difficult and require further observation as well as experimental work.

6. Conclusion

This study suggests that there has been a general increase in cover of native grass species in the semi-arid eastern part of semi-arid South Africa since 1962. This trend, which was already apparent in 1989, has continued at most locations to 2009. The increase in grass cover supports neither the degradation hypothesis of an expanding karoo shrubland (Acocks, 1953) nor the aridification hypothesis projected for the mid-21st century as a result of climate change (Ellery et al., 1991). While the pattern is clear an understanding of the key drivers of change is complex. Changes in the incidence of wet periods and perhaps a shift to an increase in early summer rainfall (Du Toit, 2010a) in the Nama-karoo biome as well as a reduction in stocking rate appear important but many other factors are likely to influence the trends in grass and shrub cover. The trajectories of change recorded in this study also support recent dynamic global vegetation models (Higgins and Scheiter, 2012) which suggest that rising temperatures and rising atmospheric CO_2 concentrations will favour grasses in the region. Large scale experiments are urgently needed to test the relative importance of such factors. Furthermore, the increase in grass cover will increase the risk of fire in the region with important consequences for vegetation structure, species composition and grazing capacity. On-going monitoring efforts over large areas are critical to document the impacts of such events on the vegetation of the region.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2014.01.011.

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