

Long-term impacts of livestock grazing in the Succulent Karoo: A 20-year study of vegetation change under different grazing regimes in Namaqualand

Elelwani Nenzhelele

Submitted in partial fulfilment of the requirements of the degree of Master of Science in Conservation Biology in the Department of Biological Sciences, University of Cape Town



Supervisors: Simon Todd & Timm Hoffman

March 2017



The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

PLAGIARISM DECLARATION

I, Elelwani Nenzhelele, declare that I have composed this thesis on my own and it has not been submitted as any part of a degree or a project anywhere else in the world. All documents that have contributed to this study have been cited and referenced in appropriate places.

Elelwani Nenzhelele (signed)

13 March 2017

Signature.....

Date.....

ACKNOWLEDGEMENTS

This MSc would have not been possible without the financial support from NRF, Wilderness Trust Fund, UCT (Percy Fitzpatrick Institute of African Ornithology and the Plant Conservation Unit).

I would like to extend my deepest gratitude to my two supervisors, Simon Todd and Timm Hoffman for your support, encouragement and input throughout this project. I am so lucky to have worked with two awesome supervisors.

Simon Todd, thank you so much for taking your time off away from work, wife and kids so that you could help me with my data collection and analysis. I appreciate all your valuable input on this project, NDOLIVHUWA!!

I would especially like to thank the co-supervisor of this project, Timm Hoffman, for not only be my supervisor but for guiding me through all my ups and down and making sure I finish this thesis on time. I couldn't have chosen a better supervisor. I did not only learn about Rangeland Ecology under your supervision but "VHUTHU" as well.

I am so grateful for Marianna Lot for assisting with my data collection in the field. There was never a dull moment working with you and listening to your stories. You taught me so much about the plants in the Succulent Karoo in just a short period.

I would especially like to thank my dear friends; Maggie for helping with my thesis especially the writing part, I am so grateful for your valuable input. To Meshack & Tendai thank for being there for me especially when I was overwhelmed and I wanted to quit. Your words of encouragement and support kept me going. Your friendship means a lot to me.

I would also like to thank the CB 2016 class for not only being my classmates but my family. Your support, jokes, words of encouragement and assistance got me through this MSc. My housemates Rozwi, Sandisiwe, Thandeka, Brunette, Tinyiko thank you for being my family away from home and for being super supportive and caring. I am so blessed with family like you.

Nobody has been more important to me than my mother TSHILIDZI. I am so grateful for your guidance in whatever I pursue. You are my number one role model and you mean the world to me. Most importantly I would like to thank my loving and supportive family, especially my

two brothers Humani and Rofhiwa for keeping me sane throughout this MSc. I love you so much and thank you for your unending support and having faith in me.



The author (left) with research assistant, Marianna Lot, in the field at Paulshoek.

Contents

PLAGIARISM DECLARATION	2
ACKNOWLEDGEMENTS.....	3
ABSTRACT.....	7
INTRODUCTION.....	9
Land use change and land degradation in the drylands.....	9
The impact of livestock grazing on semi-arid, winter-rainfall Mediterranean ecosystems..	9
Succulent Karoo: A biodiversity Hotspot	10
History of grazing regimes in Namaqualand.....	11
Dynamics of the vegetation in the Succulent Karoo.....	11
Fence-line contrast studies and change in the vegetation in Namaqualand	13
Previous findings from Paulshoek fence-line studies	14
Objectives of the study	15
METHODS.....	16
Study area	16
Data collection	18
Data analysis	21
RESULTS.....	22
Change in cover, composition and richness	22
Key shrub responses to grazing	28
Volume and size class distributions	28
Number of adult shrubs.....	32
Number of shrub seedlings.....	32
Rainfall	32
Livestock.....	35

DISCUSSION.....	36
Long-term changes (1996-2016) in cover, composition and species richness.....	36
Changes in the number and volume of key shrub species	37
Changes in the number of seedlings and plant size class distributions	38
Plant-herbivore dynamics and degradation of semi-arid rangelands	39
Implications for policy and management	40
CONCLUSIONS.....	41
REFERENCES.....	43
APPENDIX 1. Expanded description of the five indicator species used in this study.	52
<i>Galenia africana</i> L. (AIZOACEAE).....	52
<i>Ruschia robusta</i> L. Bolus (AIZOACEAE)	52
<i>Eriocephalus microcephalus</i> D.C. (ASTERACEAE)	53
<i>Tripteris sinuatum</i> D.C. (ASTERACEAE)	53
<i>Pentzia incana</i> Thunb. (Kuntze) (ASTERACEAE)	54
REFERENCES CITED IN APPENDIX 1.....	54

ABSTRACT

Livestock grazing is a key form of land-use around the world. Sustained, heavy grazing pressure, however, changes the vegetation structure of arid and semi-arid regions, often resulting in the local extinction of perennial, palatable species. It also causes changes in species composition through its impact on the recruitment of palatable and unpalatable rangeland species. Fence-line contrast studies are often used as natural experiments, since they contrast the long-term impact of herbivory between two different land tenure regimes and grazing intensities. This study used a fence-line contrast approach to investigate the long-term impact of high grazing pressure at a site in Namaqualand, South Africa.

Forty pairs of permanently marked plots, separated by a fence (with communal grazing land on one side and commercial rangelands on the other) were established in 1996 to study the long term impacts of livestock grazing. Vegetation structure and composition of the plots were analysed in 1996 and 2006. The plots were resurveyed in 2016 as part of an on-going monitoring programme in the area. The main objective of this study was to investigate changes in the vegetation structure between the overgrazed communal rangelands and the relatively lightly grazed commercial rangelands over the 20 year period.

All species in the paired plots were identified and assigned to 10 growth forms based on their height and life histories (e.g. annuals, perennials, geophytes). Differences in the average % cover as well as the number of species in each of the growth forms were compared across treatments. Differences in shrub volume, mean number of adults and the number of seedlings for each of five key indicator perennial shrub species between treatments and over time were also assessed. The five-indicator species covered a range of palatabilities from unpalatable and semi-toxic (*Galenia africana*), moderately palatable (*Ruschia robusta*, *Eriocephalus microcephalus*) and highly palatable (*Tripteris sinuatum*, *Pentzia incana*). Monthly rainfall totals and livestock grazing pressure for locations on the communal side of the fence, recorded by an on-site assistant, were also related to the changes recorded in rangeland composition over the study period.

Results indicated that there was a decline in total vegetation cover in both commercial and communal rangelands in 2016 relative to the two earlier sampling periods. The patterns observed appeared to have been influenced strongly by the reduction in annual plant cover which was especially noticeable on communal rangelands. This in turn was probably as a result of the low rainfall experienced in the seven months prior to the 2016 sampling period. The number of species in the remaining growth forms did not differ between treatments and over time. *Galenia africana* had the largest volume of the perennial shrub species although considerable variation exists between treatment and years. The average number of individuals of mature *G. africana* shrubs was significantly greater in the communal plots at all time steps. The relative patterns of abundance of the different growth forms between land use treatments were maintained across sampling periods. Continuous heavy grazing over long periods in spatially constrained grazing systems changes the vegetation from being perennial to annual-dominated. This is analogous to switching from a predictable equilibrium system with forage reserve being transferred from one year to the next to one driven more directly by seasonal rainfall. Such rangelands are more characteristic of disequilibrium systems which are more unpredictable in terms of forage supply and livestock production potential. Vulnerable people who are not buffered from economic shocks will be more severely affected by the variability in forage supply for their livestock. The impact of sustained heavy grazing over long periods of time, therefore, has important consequences for people's livelihoods.

Key words: Dryland degradation, herbivory, land-use, over-grazing, Succulent Karoo biome

INTRODUCTION

Land use change and land degradation in the drylands

Livestock grazing is a key form of land-use around the world (FAO 2004) and is the main type of land use in the drylands (Schmiedel *et al.* 2016). Grazing is, however, also seen as the main driver of biodiversity loss within such areas (Bösing *et al.* 2014). Drylands support a diverse array of plant and animal species (Chesson *et al.* 2004). They constitute 30% of the Earth's surface and support 50% of the world's livestock production (Tiejen *et al.* 2007) making them important globally. Drylands are characterised by having relatively unpredictable climates, nutrient poor soils and complex socioeconomic issues, which make them vulnerable to overgrazing and susceptible to irreversible land degradation (Schmiedel *et al.* 2016). Land degradation has been defined by the United Nations Convention to Combat Desertification as "*the reduction or loss of biological or economic productivity and complexity of terrestrial ecosystems*" (FAO 2010). The degradation of natural rangelands in dryland ecosystems caused by livestock grazing has a negative impact on the vegetation, which in turn has an impact on the livelihoods of millions of people (Adeel *et al.* 2008; Hobbs *et al.* 2008).

The impact of livestock grazing on semi-arid, winter-rainfall Mediterranean ecosystems

The impact of extensive livestock grazing is an important issue especially in the drylands of winter-rainfall Mediterranean ecosystems that are characterised by high species diversity. Occupying only 5% of the Earth's surface, Mediterranean ecosystems harbour almost 20 % of the world's vascular plants (Cowling *et al.* 1996). They also support millions of people whose livelihoods depend on the ecosystems services provided by the high biodiversity (Cuttelod *et al.* 2008).

Several studies in arid and semi-arid Mediterranean ecosystems around the world have indicated that extensive livestock grazing has altered plant composition, changed community structure, caused a decline in species diversity, and reduced soil fertility (Watkinson & Ormerod 2001; Noy-Meir & Oron 2001). In turn, this has caused a decline in ecosystem function (Tadey 2006). Arid and semi-arid Mediterranean ecosystems are sensitive to the changes in grazing pressures by livestock, since they evolved under

conditions of relatively low grazing intensity by indigenous herbivores (Kelly & Walker 1976). The high intensity of livestock grazing in the past 3000 years, however, has altered the composition of Mediterranean ecosystems (Noy-Meir & Oron 2001; Osem *et al.* 2002) and is perceived as the main factor determining the change in vegetation patterns of these areas (Naveh & Whittaker 1979; David & Goetz 1990). However, sustained heavy grazing has not been constant over either space or time in the Mediterranean regions of the world. Changes in grazing intensity over the centuries since the introduction of domestic livestock is related to socio-economic changes determined by historical events (Milchunas *et al.* 1988). According to Cingolani *et al.* (2005) it is expected that vegetation types which have evolved under low grazing intensity by indigenous herbivores will shift more in terms of their plant composition than those vegetation types which evolved under long-term, sustained grazing pressure. The latter will be more resilient to shifts in plant composition in response to herbivory (Todd & Hoffman, 1999).

Succulent Karoo: A biodiversity Hotspot

The Succulent Karoo biome is one of only two semi-arid, biodiversity hotspots in the world, with exceptional plant species endemism (Mittermeier *et al.* 2000). The Succulent Karoo is home to about 6500 vascular plants species in 1002 genera and 168 families (Cowling *et al.* 1998). Of all those plants species, 20 % occur only in the Succulent Karoo and nowhere else in the world (Driver *et al.* 2003). It is well known for having the richest dwarf succulent flora in the world (Meyers *et al.* 2000). Surprisingly, less than 8% of the biodiversity is protected (Mucina *et al.* 2006), leaving the rest under threat from climate change and land use practices.

Livestock farming is the main form of land use and provides an important source of revenue for people living in the region (Hoffman *et al.* 2007). In the communal rangelands of Southern Africa, including those in Namaqualand, overgrazing by domestic livestock has been documented as a major threat to biodiversity (Todd & Hoffman 1999). Namaqualand supports over 40% of the plant species of the Succulent Karoo biome (Cowling & Hilton-Taylor 1994). The high stocking rates in the region, particularly within the communal areas, has caused degradation of the vegetation. The long-term impacts of sustained heavy grazing, however, have not been well-documented (Todd & Hoffman 1999).

History of grazing regimes in Namaqualand

Changes in the vegetation dynamics of Namaqualand are attributed to historical changes in land use and to differences in the major land tenure systems in the area (Hoffman & Rohde 2007; Bösing *et al.* 2014). Over much of the winter rainfall region of South Africa, the vegetation was only occasionally exposed to heavy grazing pressures by indigenous herbivores (Owen-Smith *et al.* 1997; Dean & Milton 2003). In Namaqualand, domestic livestock grazing by goats, sheep, and cattle began approximately 2000 years ago with the arrival of Nama pastoralists in the region (Deacon 1992; Boonzaier *et al.* 1996). Privately-owned farms were settled by white farmers from the late 18th century onwards. Widespread fencing of these farms was initiated about 100 years later in the late 19th century. The main objective in fencing these areas was to stabilise productive output by controlling stock numbers and managing rangeland resources more effectively (Benjaminsen *et al.* 2006; Rohde *et al.* 2006). Indigenous pastoralists became increasingly marginalized and were forced to graze their herds in relatively small tracts of land owned by the church (Hoffman & Rohde 2007). Their traditional grazing regimes were disrupted and had to be altered in response to the limited land that they now had for grazing (Samuels *et al.* 2008). As a result, many people started to depend on their labour which they supplied to the mines in order to survive (Samuels *et al.* 2008). The establishment of the mission stations initiated the communal land tenure system evident today. This allowed for limited seasonal movement of people and livestock in response to climate and land use influences (Boonzaier *et al.* 1996; Rohde & Hoffman 2008). Livestock mobility is important for better management of livestock as well as to prevent a decline in the quality and quantity of forage (Samuels *et al.* 2007). Placing limits and constraints on livestock mobility in both space and time can lead to degradation (Samuels *et al.* 2008).

Dynamics of the vegetation in the Succulent Karoo

The equilibrium theory suggests that in the absence of disturbance, the vegetation of an area should be at equilibrium with the prevailing climate (e.g. rainfall and temperature) (Vetter 2005). This suggests that the species composition of an area is broadly related to the prevailing climatic conditions and that there is a climatic optimum or 'climax' vegetation condition that is possible in a particular area. Thus, it should be possible to predict the

composition of an area based primarily on its climate. In the case of rangelands, however, grazing is viewed as a form of disturbance that could have a strong influence on equilibrium conditions (Rutherford & Powrie 2009). For example, grazing could change the composition of the vegetation from being comprised of perennial and highly palatable species to annual and less palatable or even toxic species (Kelly & Walker 1976; Todd & Hoffman 1999, 2009; O'Connor *et al.* 2001). Drought is also perceived as having an effect on vegetation in a similar way to grazing and would reduce the number of perennial, palatable species in favour of shorter-lived annuals (Campbell *et al.* 2005; Vetter 2005; Todd & Hoffman 2009). However, after drought, when climatic conditions become favourable again, the vegetation would return to equilibrium conditions once more (Vetter 2005).

In contrast, the disequilibrium view suggests that the vegetation is driven by periodic droughts and is particularly relevant for semi-arid rangelands where severe drought is common (Vetter 2005; Kuiper & Meadows 2002). In this view, the number of animals kept on the veld is less important (Behnke & Scoones 1993; Scoones 1994). The theory further suggests that animal numbers seldom become high enough to impact on the vegetation due to frequent droughts which characterise most dryland environments (Kuiper & Meadows 2002). However, the disequilibrium view of rangeland dynamics has its greatest value for understanding rangelands where people are not constrained and can move over large areas to escape areas subject to drought (Hendricks *et al.* 2005; Baker & Hoffman 2006). This is seldom the case in South Africa's communal areas which are severely overcrowded and invariably enclosed with fences, (Samuels *et al.* 2007).

Prior to the colonial era, Nama pastoralists occupying Namaqualand moved their livestock over hundreds of kilometres within large transhumance cycles in search of better grazing for their livestock particularly during periods of severe drought (Hoffman & Rohde 2007). However, extensive mobility is no longer possible in Namaqualand due to the fact that people are constrained to particular areas, which limits the amount of land available for their livestock (Samuels *et al.* 2007). This has resulted in there being sustained heavy grazing pressure on Namaqualand's communal rangelands. This has led to the transformation of the vegetation in terms of its structure, composition and function (Todd & Hoffman 1999, 2009; Anderson & Hoffman 2007).

Fence-line contrast studies and change in the vegetation in Namaqualand

In arid and semi-arid regions, the effects of grazing management on natural communities of long-lived plants generally take decades to become apparent (Wiegand & Milton 1996). Long-term studies are therefore important for understanding the major influences on the vegetation. The impact of livestock grazing on rangeland biodiversity has been addressed in several studies (Hanke *et al.* 2014). However, the majority of these studies has been relatively short-term and carried out on privately-owned farms although several long-term studies have been undertaken on experimental agricultural stations such as in Carnarvon and Grootfontein, Middelburg. There is still a lack of empirical evidence from long-term studies on the impact of grazing on the biodiversity of communal rangelands.

In this regard, fence-line contrast studies are often used as natural experiments, since they contrast the long-term impact of herbivory between two different land tenure regimes (communally-owned versus privately-owned) and grazing intensities (Asner *et al.* 2004; Diaz *et al.* 2007; Rutherford *et al.* 2012). This approach has been widely followed in Namaqualand in the last few decades. Several fence-line contrast studies have compared the effects of different grazing regimes on the vegetation of the region (Anderson & Hoffman 2007; Todd & Hoffman 1999, 2009; Petersen *et al.* 2004; Vetter 2005).

Results from these studies suggest that different grazing intensities in the Succulent Karoo biome affect vegetation types differently. For example, no change in species richness was recorded under the relatively heavy grazing regimes practiced in communal areas relative to lightly grazed commercial farms by (Todd & Hoffman 1999; 2009; Anderson & Hoffman 2007; Haarmeyer *et al.* 2010). Hendricks *et al.* (2005), however, reported a decline in species richness in areas where intense grazing had occurred. An increase in species richness due to heavy grazing has also been noted (Rutherford & Powrie 2010) primarily as a result of an increase in annual species.

In many grazing systems of the world's drylands, long-term, sustained heavy grazing has been shown to increase species richness by favouring relatively small-seeded annual species (Dreber & Elser 2011). For Namaqualand, Simons & Allsopp (2005) also reported a change in species composition from perennials to annual growth forms in response to heavy grazing. There also appears to be a general trend for an increase in unpalatable and semi-toxic

species in areas where sustained heavy grazing has been experienced (Petersen *et al* 2004; Todd & Hoffman 2009). In Namaqualand, one of the most important species in this regard is the unpalatable and semi-toxic species, *Galenia africana* which frequently increases in highly disturbed locations (Riginos & Hoffman 2003).

Several similar studies in the world's drylands have looked at the impact of livestock grazing under contrasting land tenure regimes (Todd & Hoffman 1999; 2009; Noy-Meir & Oron 2001). The results indicate that sustained heavy grazing alters plant composition structure, and causes a decline in species diversity and soil fertility. It also appears to favour the recruitment of unpalatable woody species over palatable species (Noy Meir & Oron 2001; Olsvig-Whittaker *et al.* 1993; Tadey 2006). Long-term data sets are valuable for assessing year-to-year variability in important vegetation parameters and their temporal trends (Milchunas *et al.* 1994).

Previous findings from Paulshoek fence-line studies

One of the first fence-line contrast studies undertaken in Namaqualand was initiated in 1996 (Todd & Hoffman 1999). This study compared the species richness and community composition between-heavily grazed communal rangeland in Paulshoek and lightly grazed, neighbouring, privately-owned farms (hereafter referred to primarily as commercial rangelands). The key findings of this study indicated that while there was no difference in overall plant species richness, there was a decrease in the number of large palatable shrub species in the communal lands. The communal rangelands were also associated with greater annual and geophyte species richness while the commercial rangelands were associated with greater succulent and perennial shrub richness. There was also little recruitment of the palatable shrub species in the communal compared to the commercial rangelands (Todd & Hoffman 1999). These results support those which have been undertaken elsewhere in the Succulent Karoo (Milton 1995). A general finding is that continuous heavy grazing in the communal rangelands results in an increase in annuals as well as an increase in unpalatable perennial growth forms whilst causing a decline in the cover and biomass of especially palatable, leaf succulent, perennial plants (Anderson & Hoffman 2007).

In 2006, a second study was undertaken in Paulshoek using the same, permanently marked plots that were examined in 1996. The plots were resurveyed in order to determine what

further changes had occurred in the vegetation across the fence-line between the two land-use systems (Todd & Hoffman 2009). This follow-up study found that the relative extent of plant community divergence had been maintained over the 10-year period. However, some recruitment of palatable shrub species had occurred in the communal rangeland, demonstrating the potential for the recruitment of useful rangeland species following good rainfall events even under high grazing pressure (Todd & Hoffman 2009). The results of this long-term study in Namaqualand confirm Hanke *et al.*'s (2014) findings that over-grazing alters the functional structure of the vegetation. The results also suggest that changes in functional structure can be maintained for a decade or even longer.

This thesis builds on the previous studies undertaken by Todd and Hoffman (1999, 2009), by adding an additional sampling period 20 years after the initial survey. Taken together, these three studies provide one of the longest records of the impacts of heavy grazing on the vegetation of the Succulent Karoo biome. Communal area farmers from Namaqualand are in the process of expanding their land holdings through the on-going land redistribution programmes in the area. This study, therefore, forms an important baseline for land reform policy in the region and will highlight the potential consequences of heavy grazing for the vegetation of Namaqualand. The results from this study can also be used by land owners to make informed decisions about the management of their natural assets. The work will also attract more researchers into long-term monitoring studies, similar to this one.

Objectives of the study

The study has the following objectives:

- To investigate long-term (1996 -2016) changes in plant species richness and the composition and cover of different growths forms in heavily-grazed communal rangelands and lightly-grazed commercial rangelands in order to determine if the responses observed between 1996 and 2006 are consistent with those for the period 2006-2016.
- To examine the changes in five key shrub species (including palatable and unpalatable species) over 20 years.
- To interpret the results of the study in relation to known arid land, plant-herbivore dynamics.

- To explore the implications for policy makers in the land reform, land management and conservation sectors.

METHODS

Study area

The study area is located in central Namaqualand in the Leliefontein communal area and adjacent privately-owned farms. Data collection was restricted to locations within the 20 000 ha of communal rangeland used by people within the village of Paulshoek and the five privately-owned, commercial farms which surround the communal area (Petersen *et al.* 2004). Namaqualand is a winter rainfall region which receives 150 mm - 250 mm rainfall per annum, most of which falls in the period June-August (Cowling *et al.* 1998). Frequent droughts characterize the area but usually do not last more than a year (Desmet 2007). The geology of the region is characterised by metamorphosed gneiss which forms distinctive granite hills separated by sandy plains (Cowling *et al.* 1998). While the highest peaks in the region are over 1700 m the elevation of sites in the study area are between 900-1000 m asl.

The flora of this region is unique. Leaf succulent shrubs in the families Aizoaceae, Crassulaceae, and Euphorbiaceae dominate the vegetation on the sandy plains (Desmet 2007). The rocky hills are characterized by a higher proportion of non-succulent shrubs represented mainly by species within the family Asteraceae (Anderson & Hoffman 2007). *Ruschia robusta* is a succulent shrub which dominates the privately-owned farms. The more heavily disturbed and trampled areas in the communal rangelands are dominated by the relatively unpalatable, semi-toxic shrub, *Galenia africana*. This species can invade heavily disturbed areas such as around kraal sites where a gradient of disturbance away from the central location is often apparent (Riginos & Hoffman 2003). During the spring months (Aug-Oct) and particularly after good winter rains, annuals and geophytes provide a mass display of colour which attracts visitors to the region (Desmet 2007).

The main form of land use in the study area is small stock farming of sheep and goats (Petersen *et al.* 2004). Grazing regimes in the Paulshoek communal lands are characterised by a large number of sheep and goats foraging around the same central stock post each day.

Recommended stocking rates for the area, and which are provided by the Department of Agriculture, are about 12 ha per small stock unit (SSU) (van den Berg 1983). For the past 40 years, the mean stocking rates on the communal rangelands of South Africa, in general, have been up to 1.85 times higher than this (Hoffman & Ashwell 2001). Similarly-high stocking rates have been recorded in Namaqualand (Anderson & Hoffman 2007). As a result, grazing is continuous over large parts of the communal area. This limits forage growth rates, often resulting in a decline in forage availability, particularly during drought conditions. Continuous heavy grazing can also have a negative impact on the quality of the animals, which are sold locally for domestic consumption but also commercially, particularly before the major festive periods such as Christmas and Easter.

In contrast to the Paulshoek communal rangelands, herds on the commercially-managed rangelands (hereafter referred to as 'commercial rangelands') are usually owned by a single owner and are comprised of high quality mutton sheep (Dorpers) which are sold commercially to markets. Unlike in the communally-managed rangelands (hereafter referred to as 'communal rangelands'), sheep in the commercial rangelands are not herded on a daily basis but are allowed to graze freely in fenced paddocks. Animals are also rotated between paddocks providing the vegetation some rest from grazing. This facilitates forage regrowth, increases productivity and also increases the nutrients in the soil (Samuels *et al.* 2007). The effects on the vegetation of the different stocking rates and management regimes between communal and commercial rangelands are clearly evident in Paulshoek along fence lines which separate the different land tenure regimes (Figure 1).



Figure 1. The effect of different grazing regimes in Namaqualand is clearly evident along fence-lines which separate communal rangelands (left) from commercial rangelands (right).

Data collection

The same procedure undertaken in the 1996 and 2006 fence-line studies (Todd & Hoffman 1999, 2009) was followed when collecting the data in 2016. Data were collected from the same 40 permanently-marked pairs of plots separated by a fence, with commercial rangelands on one side and communal rangelands on the other (Figure 2). Thus, a total of 80 plots were sampled. Each plot was at least 10 m away from the fence to avoid edge effects created by the presence of the fence and to minimize habitat heterogeneity. The 10 x 10 m plots are located over a distance of 20 km along the fence, in roughly 100 m intervals. GPS coordinates recorded during the two previous studies were used to locate the exact position of the plots which have been marked with metal stakes and small rock cairns to assist in relocating their position. Metal tags were also placed on the fence after the first sampling in 1996 to mark the position of each pair of plots. This enabled the plots which were sampled in 2016 to be laid out in the exact position they were in 1996 and 2006.

All the data for this study were collected in the last two weeks of September 2016 with the help of the same person (Simon Todd) who collected the data for the 1996 and 2006 studies. This reduced the degree of observer bias inherent in studies of this nature. All

plants occurring in the plots were identified to species level and their percent cover was estimated visually. In addition, the height and average width of the same five indicator shrub species which were sampled in 1996 and 2006 were measured in 2016. All individuals in the plots were measured up to a maximum of 32 individuals per plot. These five indicator species are the most abundant in the area and range from being relatively unpalatable and semi-toxic to livestock (*Galenia africana*), to being moderately palatable (*Ruschia robusta*, *Eriocephalus microcephalus*) or highly palatable (*Tripteris sinuatum*, *Pentzia incana*). Further details on each of these species are provided in Appendix 1.



Figure 2. Data being collected in one of the 10x10 m plots on the commercial rangeland at Rooiwal.

The number of adult and young plants of species with different palatabilities can often reflect the degree of herbivore impact on rangelands (Anderson and Hoffman 2007). To investigate this, the number of adult plants as well as the number of seedlings (individuals <10 cm in height) of each of the five-indicator species was counted in the plots on both the

commercial and communal rangelands. Comparisons for the seedling data, however, was only available for the 1996 sample as the number of seedlings was not recorded in 2006.

The volume of the five-indicator species was calculated using the height and the diameter of individuals. Each plant was represented as an oblate spheroid using the formula below (Philips and McMahon 1981) where V is the volume (in cm^3), and a represents the minor axis (height or diameter, whichever is smaller) and b the major axis (height or diameter, whichever is larger):

$$V = (\pi a^2 b) / 6$$

Rainfall data for the period 1996-2016 were averaged for three locations in the study area (Paulshoek village, Kleinfontein, Slooitjiesdam) where standard funnel rainfall gauges have been in place for most of the study period. Values for the first eight months of 1996, however, were not available and the monthly values for Springbok, 90 km to the north of Paulshoek were therefore used. There is a significant correlation between monthly rainfall totals for Paulshoek and those for Springbok (unpublished data). The long-term average for both locations is about 200 mm most of which falls in the winter months (Apr-Aug). Despite this similarity, however, the record for the period before September 1996 should be seen as being indicative of the actual value only.

The number of sheep and goats found in stock posts within 2 km of the survey plots were counted each month from 1998 onwards. The 2 km limit used in this study represents the average distance that a herd grazes from the stock post each day (Samuels 2008). The total number of animals in each of the relevant stock posts was added together each month to provide a relative measure of the grazing pressure on the communal rangelands. For the commercially-managed farms it was assumed after three years of close contact with the farmers utilising these adjacent properties that livestock numbers were kept in accordance with the relatively conservative values recommended by the Department of Agriculture, Land Reform and Rural Development. Monthly observations in the field over the duration of the study period and independent values collected over a two-year period in the early 2000s suggests that this is a reasonable assumption (MT Hoffman, unpublished data).

Data analysis

All species were identified and assigned to 10 growth forms based on their height and life histories (Cornelissen *et al.* 2003). The 10 growth forms were annuals, annual grasses, perennial grasses, perennial forbs, geophytes, dwarf woody shrubs, woody shrubs, dwarf succulents, dwarf succulent shrubs, and succulent shrubs. These are the same categories that were used by Todd & Hoffman (1999, 2009). Differences in the average % cover as well as the number of species in each of the growth forms was compared across treatments (commercial and communal rangelands) and over time (1996, 2006, 2016) using a Kruskal-Wallis one-way ANOVA and Dunn's multiple comparison tests with a Bonferroni correction applied (Corder *et al.* 2009). The Bonferroni correction was applied in order to reduce the chance of obtaining a false positive (type I errors) when multiple pairwise tests are performed on a single dataset. Differences in total values for the cover and species richness of annuals, perennials and all growth forms combined were also assessed across treatments and over time using the same approach indicated above. XLSTAT (version 19.01) was used for the statistical analyses (Addinsoft 2017).

Differences in shrub volume for each of the five indicator perennial shrub species between treatments and over time were assessed using a separate t-test assuming unequal variances. Changes in the size class distribution of the five indicator shrub species on both sides of the fence at each time step were also graphed using the volume estimates for individuals. Differences in the mean number of individuals of adults and seedlings of the five indicator perennial shrub species between commercial and communal plots over time were assessed using a separate t-test assuming unequal variance.

RESULTS

Change in cover, composition and richness

There was a decline in total vegetation cover in both commercial and communal rangelands in 2016 relative to the two earlier sampling periods (Table 1 & Figure 3). This decline was influenced strongly by the reduction in annual plant cover which was especially noticeable on the communal rangeland. Changes in perennial plant cover also affected the total cover of vegetation over the sampling period. The cover of individual perennial growth forms, such as dwarf woody shrubs, succulent shrubs and woody shrubs did not change substantially over the sampling period. However, there was an overall decline in perennial plant cover in 2016 relative to 1996. This is especially apparent within commercial rangelands, where perennial growth forms comprised a larger proportion of the cover.

Because of the high variation in the % annual cover among plots there were few significant differences in the cover of annuals between commercial and communal areas for the period 1996 and 2006 (Table 1 & Figure 3). However, in 2016 average % cover values for annuals (e.g. *Wahlenbergia prostrata*, *Lysera tenella*) were significantly lower for both treatments compared to previous sampling periods. The cover of annual grasses (e.g. *Pentaschistis spp.*, *Karoochloa schismoides*) was low (<2%) throughout the sampling period but was highest in 1996, especially in the communal plots, and lowest in 2016. The cover of dwarf woody shrubs such as *Hirpicium alienatum* and *Pentzia incana* was generally higher for plots on the commercial side of the fence but was relatively stable within each treatment over time. Perennial forbs (the most common of which was *Gazania heterochaeta*) rarely comprised more than 1% cover and did not differ significantly between 1996 and 2016. The cover of geophytes (e.g. *Moraea serpentina*, *Oxalis obtusa*) was highest in 2006 for both commercial and communal areas but rarely comprised more than 1% of the total cover.

Table 1. Mean % vegetation cover (\pm SE) for 40 paired plots in commercial and communal rangelands sampled over three periods for 10 different growth forms. Different superscripts within a growth form denote significant differences based on a Kruskal-Wallis one-way ANOVA and Dunn's multiple comparison test with a Bonferroni correction applied. The absence of superscripts indicates that no significant differences were found between commercial and communal areas over the sampling period.

Growth form	% cover (1996)		% cover (2006)		% cover (2016)	
	Commercial	Communal	Commercial	Communal	Commercial	Communal
Annuals	5.7 \pm 0.7 ^{ab}	16.2 \pm 2.4 ^a	3.2 \pm 0.4 ^b	9.2 \pm 1.4 ^{ab}	0.2 \pm 0.0 ^c	1.0 \pm 0.2 ^c
Annual grasses	1.0 \pm 0.5 ^a	1.7 \pm 0.51 ^{ab}	0.1 \pm 0.0 ^{bc}	0.3 \pm 0.0 ^{cd}	0.0 \pm 0.0 ^{de}	0.1 \pm 0.0 ^e
Dwarf woody shrubs	6.4 \pm 0.2 ^a	2.9 \pm 0.6 ^b	4.3 \pm 0.5 ^{ab}	2.5 \pm 0.3 ^{ab}	3.4 \pm 0.5 ^{ab}	2.3 \pm 0.3 ^b
Dwarf succulents	2.5 \pm 1.0	1.1 \pm 0.3	1.8 \pm 0.6	0.9 \pm 0.2	1.6 \pm 0.4	1.1 \pm 0.3
Dwarf succulent shrubs	2.5 \pm 0.8	1.1 \pm 0.3	1.8 \pm 0.5	1.5 \pm 0.3	1.4 \pm 0.3	0.2 \pm 0.2
Perennial forbs	0.2 \pm 0.1 ^a	0.5 \pm 0.2 ^{ab}	0.2 \pm 0.0 ^{ab}	0.5 \pm 0.0 ^b	1.0 \pm 0.2 ^a	0.2 \pm 0.1 ^{ab}
Geophytes	0.5 \pm 0.2 ^c	0.7 \pm 0.2 ^c	0.8 \pm 0.0 ^{ab}	1.2 \pm 0.1 ^a	0.3 \pm 0.0 ^c	0.7 \pm 0.1b ^c
Perennial grass	1.1 \pm 0.4	1.1 \pm 0.6	0.4 \pm 0.2	0.4 \pm 0.2	0.4 \pm 0.1	3.0 \pm 0.1
Succulent shrubs	24.3 \pm 2.6 ^a	16.5 \pm 3.2 ^b	15.5 \pm 1.6 ^{ab}	10.6 \pm 1.9 ^b	13.7 \pm 1.2 ^{ab}	9.9 \pm 1.7 ^b
Woody shrubs	7.8 \pm 1.2	6.5 \pm 1.2	6.7 \pm 0.7	6.5 \pm 1.2	6.2 \pm 1.6	4.5 \pm 0.6
Total Annuals cover	7.2 \pm 0.9 ^{bc}	18.6 \pm 2.8 ^a	4.1 \pm 0.4 ^c	10.7 \pm 1.5 ^{ab}	0.6 \pm 0.1 ^d	1.8 \pm 0.3 ^d
Total Perennials cover	45.0 \pm 2.0 ^a	29.4 \pm 2.8 ^{bc}	30.9 \pm 1.4 ^b	22.8 \pm 1.7 ^c	26.8 \pm 1.0 ^{bc}	19.3 \pm 1.6 ^c
Total Vegetation cover	52.2 \pm 2.0 ^a	48.1 \pm 3.0 ^{ab}	35.1 \pm 1.3 ^{bc}	33.5 \pm 1.8 ^{cd}	27.3 \pm 1.0 ^{de}	21.1 \pm 1.4 ^e

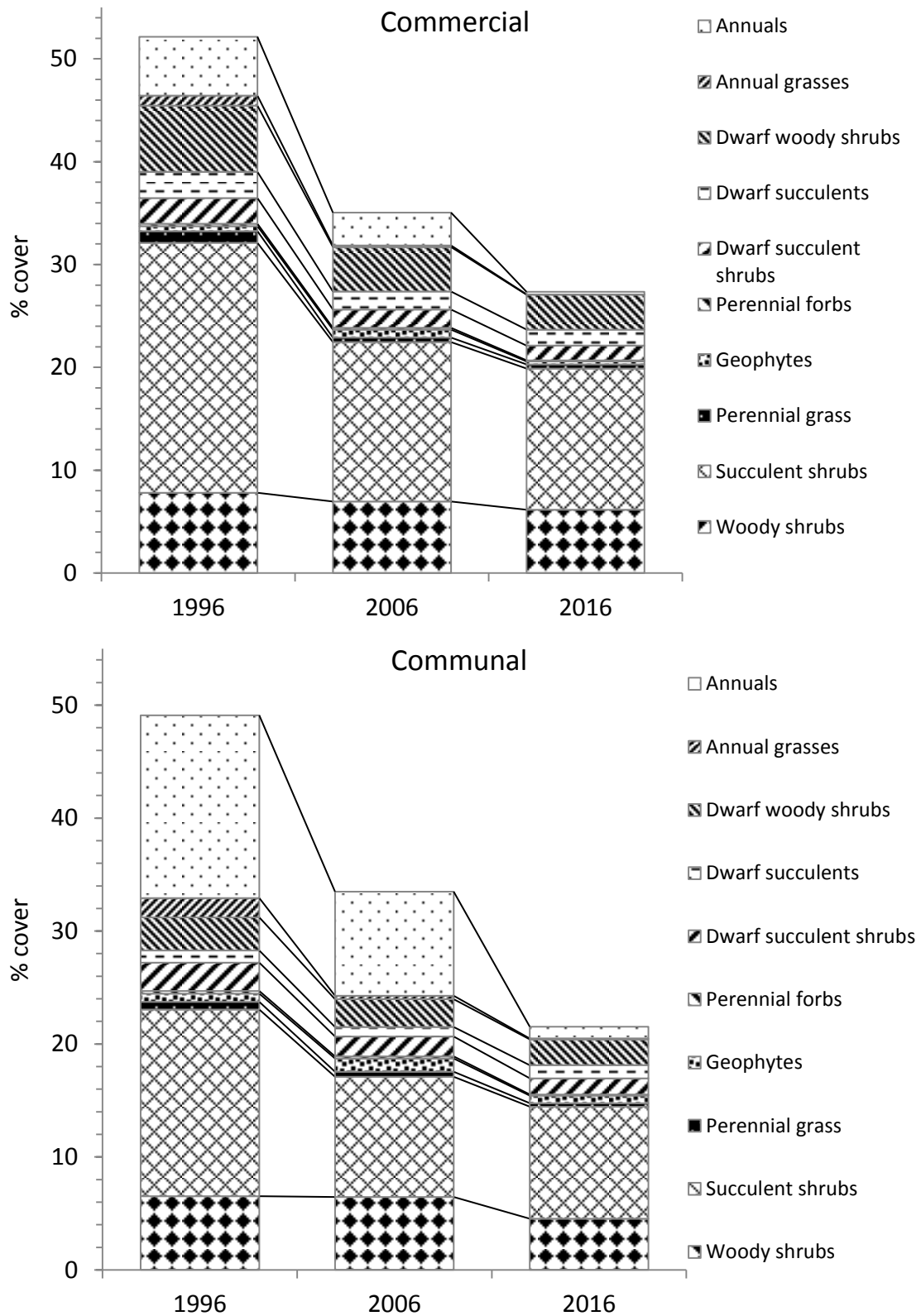


Figure 3. The % cover of each growth form in the commercial (top) and communal (bottom) rangelands in each of the sampling periods (1996, 2006, 2016).

In every sampling period, in both commercial and communal plots, the average % cover for succulent shrubs such as *Ruschia robusta* and *Leipoldtia schultzei*, comprised the highest cover value. Within each treatment, however, the average value for succulent shrub cover did not decline significantly over the study period. There were no significant differences in the % cover across treatments and years for the remaining growth forms including dwarf succulents (e.g. *Cheiridopsis* spp., *Cephalophyllum ebracteatum*), dwarf succulent shrubs (e.g. *Drosanthemum hispidum*, *Hypertelis salsoloides*), perennial grasses (e.g. *Stipagrostis zeyheri*, *Chaetobromus involucratus*) and woody shrubs (e.g. *G. africana*, *E. microcephalus*).

The total cover of annuals (annuals, annual grasses and geophytes) was significantly lower in 2016 when compared to other sampling periods (Table 1, Figure 3). While geophytes are perennial they function as annuals as they only appear above the ground for a brief part of the year and are therefore not available for livestock. The highest values for annual plant cover were recorded on the communal rangelands in 1996 and values were generally higher on communal than commercial rangelands. In contrast, values for perennial plant cover were higher in commercial plots and decreased on both sides of the fence over the sampling period. Total vegetation cover was significantly higher in 1996 in both treatments than in 2016. Values were not significantly different between treatments at each time step but were significantly different within the same treatment over time. Values for the communal plots at the earlier time step did not differ significantly with values from the commercial plots at the later time step.

Values for the number of annuals and annual grass species were relatively similar between treatments in 1996 and 2016 (Table 2 & Figure 4). However, the highest number of annual and annual grass species was recorded in 2006 in the communal plots while the lowest number of annual species for both growth forms and in both treatments occurred in 2016. There were only 1 or 2 perennial forbs species during all sampling periods but this number was highest in the communal plots in 2006. The number of geophyte species in both commercial and communal plots was significantly higher in 2006 than in the other two sampling periods. The number of succulent shrub species was generally higher in commercial plots and did not differ within each treatment over the sampling period. The number of species in the remaining growth forms did not differ between treatments and over time.

Table 2. Mean (\pm SE) number of species in each of 10 growth forms in 40 paired plots sampled in commercial and communal rangelands over three periods. Different superscripts within a growth form denote significant differences based on a Kruskal-Wallis one-way ANOVA and Dunn's multiple comparison test with a Bonferroni correction applied. The absence of superscripts indicates that no significant differences were found between commercial and communal areas over the sampling period.

Growth form	No. species (1996)		No. species (2006)		No. species (2016)	
	Commercial	Communal	Commercial	Communal	Commercial	Communal
Annuals	10.8 \pm 0.5 ^b	12.7 \pm 0.5 ^{ab}	13.9 \pm 0.7 ^{ab}	16.9 \pm 0.6 ^a	2.3 \pm 0.4 ^c	4.0 \pm 0.5 ^c
Annual grass	1.0 \pm 0.1 ^{ab}	1.4 \pm 0.2 ^a	0.9 \pm 0.1 ^{ab}	1.5 \pm 0.1 ^a	0.3 \pm 0.1 ^c	0.6 \pm 0.1 ^{bc}
Dwarf woody shrubs	4.6 \pm 0.3	4.5 \pm 0.3	5.03 \pm 0.4	5.2 \pm 0.3	4.6 \pm 0.3	5.1 \pm 0.4
Dwarf succulents	1.9 \pm 0.2	2.9 \pm 0.2	2.2 \pm 0.3	1.9 \pm 0.3	1.9 \pm 0.3	1.7 \pm 0.2
Dwarf succulent shrubs	3.3 \pm 0.2	4.4 \pm 0.3	3.5 \pm 0.2	3.3 \pm 0.3	2.9 \pm 0.2	2.8 \pm 0.2
Perennial forbs	1.4 \pm 0.1 ^{ab}	1.4 \pm 0.4 ^{ab}	1.4 \pm 0.2 ^{ab}	1.7 \pm 0.2 ^a	1.0 \pm 0.2 ^b	1.1 \pm 0.2 ^{ab}
Geophytes	3.3 \pm 0.4 ^b	4.2 \pm 0.4 ^b	7.0 \pm 0.5 ^a	9.0 \pm 0.7 ^a	2.8 \pm 0.3 ^b	4.7 \pm 0.6 ^b
Perennial grass	0.8 \pm 0.1	1.8 \pm 0.2	1.0 \pm 0.2	1.0 \pm 0.2	1.8 \pm 0.1	0.9 \pm 0.2
Succulent shrubs	3.6 \pm 0.3 ^{ab}	2.4 \pm 0.3 ^c	3.8 \pm 0.3 ^{ab}	2.8 \pm 0.3 ^{bc}	3.9 \pm 0.2 ^a	2.8 \pm 0.3 ^{bc}
Woody shrubs	5.0 \pm 0.3	4.5 \pm 0.1	5.3 \pm 0.3	4.8 \pm 0.3	5.2 \pm 0.2	4.8 \pm 0.3
Total Annuals	15.0 \pm 0.7 ^{cd}	18.3 \pm 0.7 ^{bc}	21.7 \pm 0.9 ^{ab}	27.3 \pm 1.1 ^a	5.2 \pm 0.7 ^e	9.2 \pm 1.0 ^{de}
Total Perennials	20.5 \pm 0.8 ^{ab}	18.2 \pm 0.9 ^b	22.4 \pm 0.8 ^a	20.7 \pm 0.9 ^{ab}	20.3 \pm 0.7 ^{ab}	19.7 \pm 0.8 ^{ab}
Total Species Richness	35.5 \pm 1.0 ^c	36.6 \pm 1.1 ^{bc}	44.1 \pm 1.5 ^{ab}	48.8 \pm 1.5 ^a	24.5 \pm 1.1 ^d	28.3 \pm 1.4 ^d

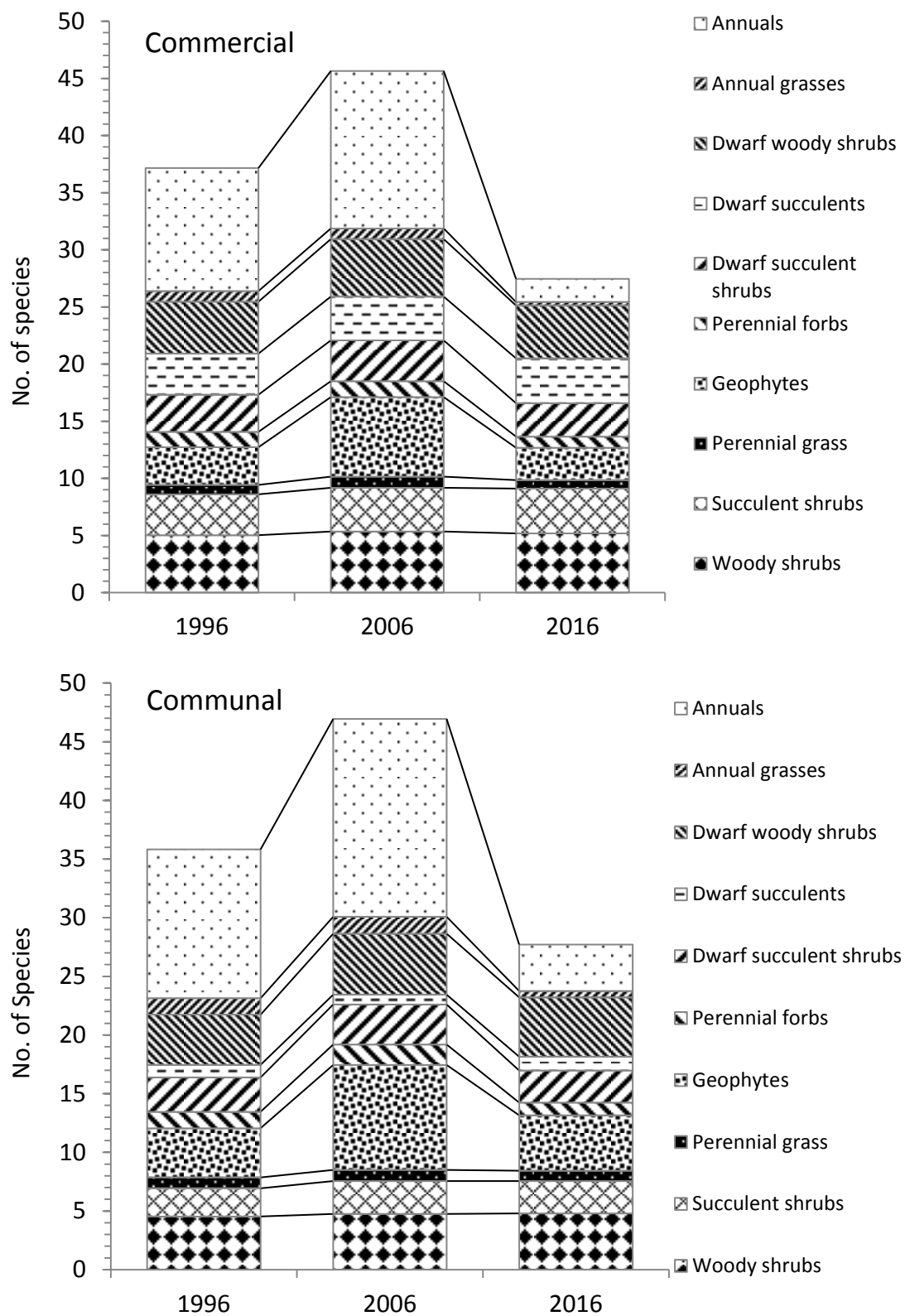


Figure 4. The number of species in each growth form in the commercial (top) and communal (bottom) rangelands in each of the sampling periods (1996, 2006, 2016).

The total number of species recorded as annuals (including annuals, annual grasses and geophytes) was lowest in 2016 and highest in 2006 (Table 2, Figure 4). The total number of perennial species did not differ between treatments at each time step and remained within a relatively narrow range of between 18.2 and 22.4 species per 10 x 10 m plot. Total species richness was influenced by the number of annual species and was highest in 2006 and lowest in both treatments in 2016.

Key shrub responses to grazing

Volume and size class distributions

Of the five shrub species measured in this study *Galenia africana* had the largest volume, although considerable variation exists between treatment and years (Table 3, Figure 5). *G. africana* shrub volumes were not significantly different between commercial and communal plots in 1996 and 2016 but were significantly lower in communal plots in 2006. The volume of *Ruschia robusta* shrubs was significantly greater in commercial plots in 1996 and 2006 although differences were not significantly different between treatments in 2016. For the remaining three more palatable shrub species (*Eriocephalus microcephalus*, *Tripteris sinuatum* and *Pentzia incana*) shrub volumes were significantly lower in communal plots in all three sampling periods. For the two most palatable species (*T. sinuatum* and *P. incana*) the difference in volume between plants in commercial and communal plots was striking.

The size class distributions of the five shrub species are shown in Figure 6. There were more small plants in commercial plots for all species and at all time steps except for *Galenia africana*. For this species, the number of small plants was greater on the communal side of the fence, especially in 2006. In general, data for 2006 showed the greatest number of small plants in all species than any other year. Although there were small plants of palatable species on the communal side of the fence at all times steps their growth and transition to larger individuals was low. In all three sampling periods, the commercial side of the fence was characterised by the recruitment of more seedlings of palatable shrub species that survived to adulthood than the communal plots.

Table 3. Average volume ($\times 10^3 \text{ cm}^3$) ($\pm \text{SE}$) of five shrub species in 40 paired plots on commercial and communal rangeland at three sampling periods. P-values show the level of significance following a t-test comparing the volume of each species in commercial and communal rangelands at each time step.

Species	Shrub volume ($\times 10^3 \text{ cm}^3$)											
	(1996)				(2006)				(2016)			
	Commercial	Communal	df	p	Commercial	Communal	df	p	Commercial	Communal	df	p
<i>Galenia africana</i>	82 \pm 8	100 \pm 6	246	NS	46 \pm 8	31 \pm 2	198	0.004	50 \pm 6	69 \pm 5	160	NS
<i>Ruschia robusta</i>	37 \pm 2	18 \pm 2	920	0.001	19 \pm 1	15 \pm 1	677	0.013	32 \pm 2	27 \pm 2	757	NS
<i>Eriocephalus microcephalus</i>	42 \pm 3	18 \pm 3	208	0.001	24 \pm 1	15 \pm 2	297	0.001	42 \pm 3	30 \pm 4	358	0.001
<i>Tripteria sinuatum</i>	41 \pm 6	5 \pm 1	192	0.001	18 \pm 2	3 \pm 0	255	0.001	30 \pm 3	6 \pm 1	428	0.001
<i>Pentzia incana</i>	27 \pm 3	8 \pm 1	149	0.001	15 \pm 1	6 \pm 0	213	0.001	18 \pm 2	7 \pm 2	233	0.001

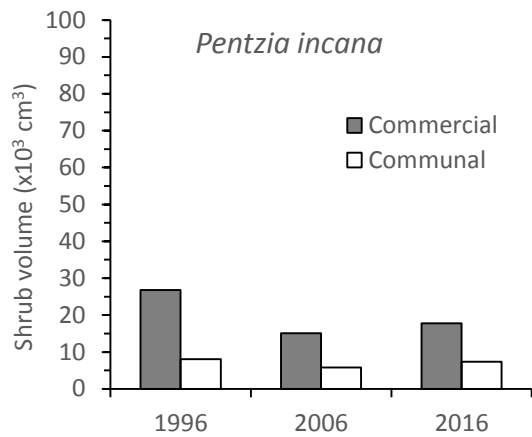
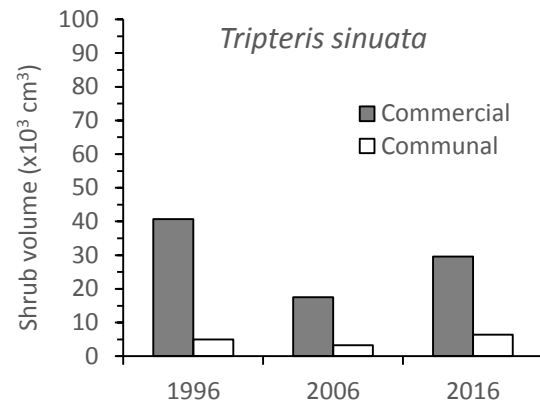
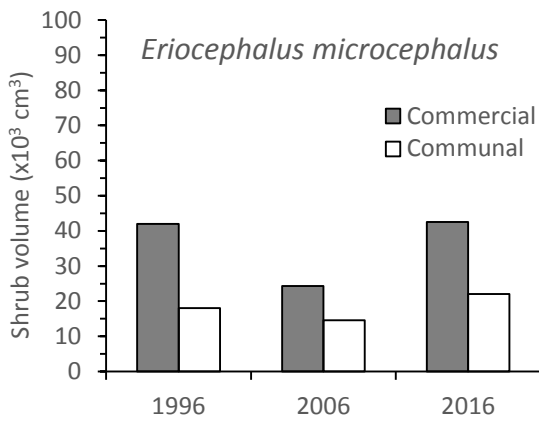
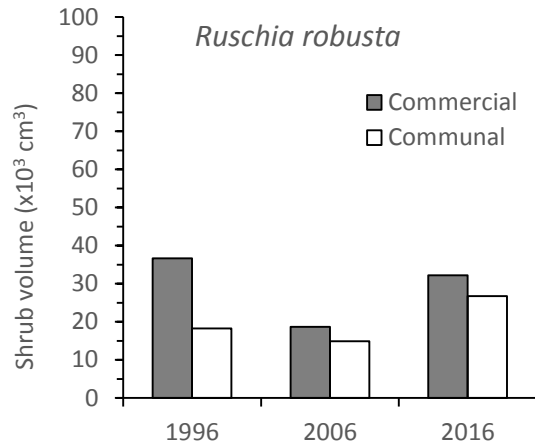
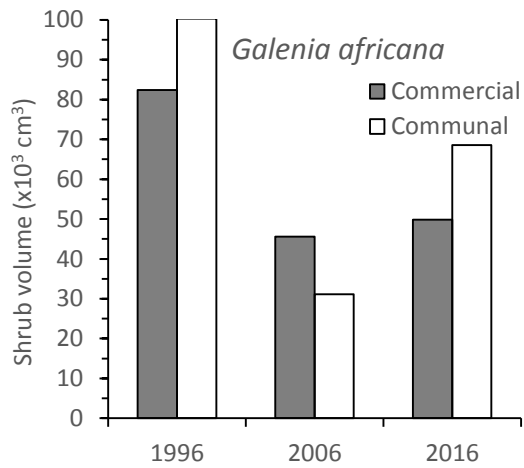


Figure 5. The average volume (x10³ cm³) of five shrub species between three different time periods in commercial and communal rangelands in each of the sampling periods (1996, 2006, 2016).

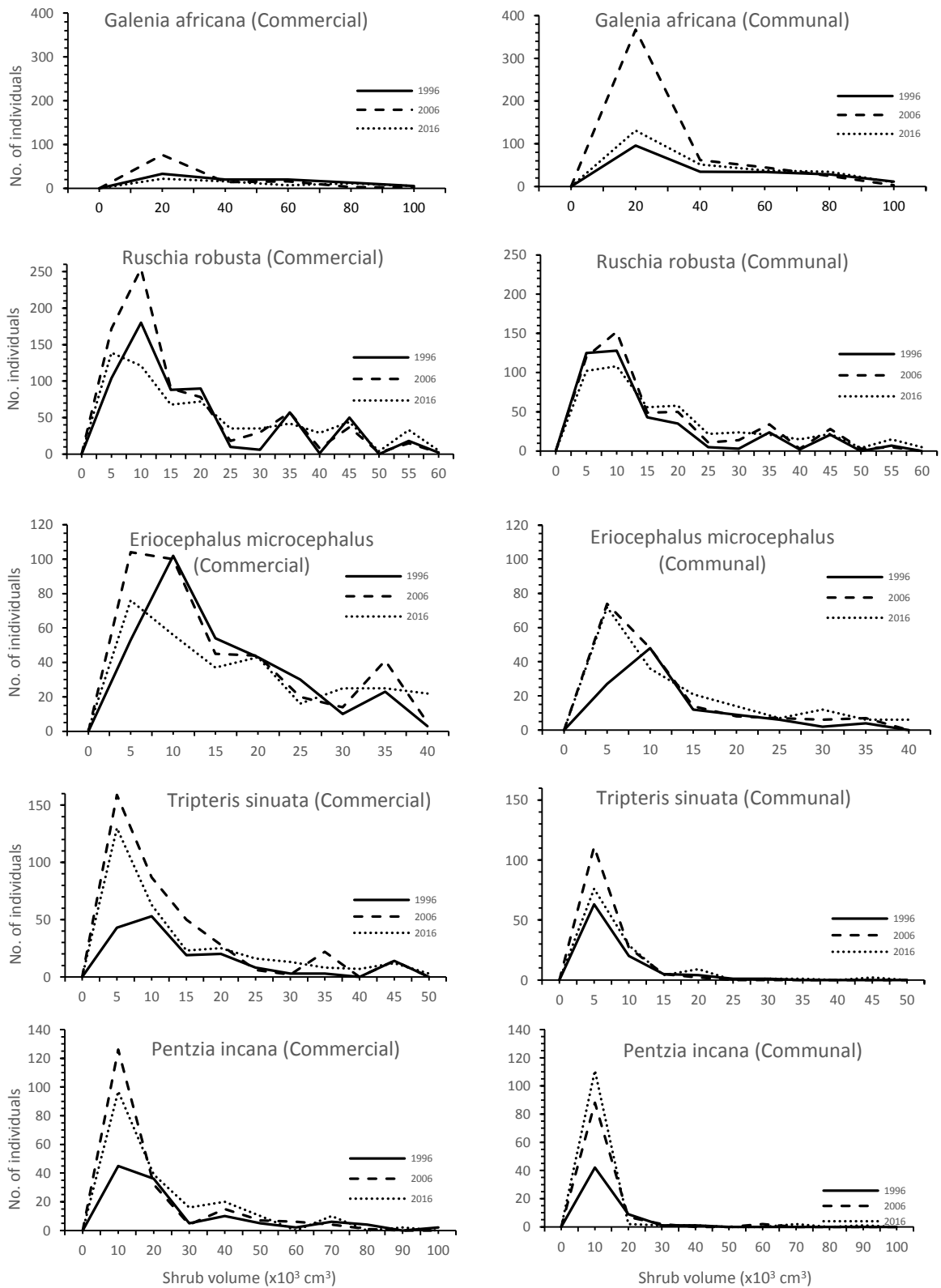


Figure 6. Shrub volume ($\times 10^3 \text{ cm}^3$) size class distributions for the number of individuals of *Galenia africana*, *Ruschia robusta*, *Eriocephalus microcephalus*, *Tripteris sinuatum* and *Pentzia incana* in commercial and communal areas for the periods 1996, 2006 and 2016.

Number of adult shrubs

The average number of individuals of mature *Galenia africana* shrubs was significantly higher in the communal plots at all time steps (Table 4). The number of adult *Ruschia robusta* shrubs was significantly higher in the commercial plots in 1996 and 2016 but not in 2006. The number of adult *Eriocephalus microcephalus* and *Tripteris sinuatum* individuals was significantly higher in commercial plots at all time steps (1996, 2006 and 2016). The number of individuals of the palatable shrub species *Pentzia incana* was also highest in commercial plots although not significantly so in 1996 and 2006. The number of individuals of both *T. sinuatum* and *P. incana* was lowest in 2016 within both treatments.

Number of shrub seedlings

The number of seedlings of *G. africana* was significantly higher in the communal plots in both 1996 and 2016 (Table 5). Differences in the number of seedlings of this species (*G. africana*) between commercial and communal rangelands were substantially higher in 2016 relative to 1996. Differences in the number of seedlings of the remaining species in commercial and communal plots were significantly different in 1996 but not in 2016. The number of seedlings of *Ruschia robusta*, *Eriocephalus microcephalus* and *Tripteris sinuatum* were generally lower in 2016 compared to 1996, particularly in commercial rangelands.

Rainfall

Rainfall over the period 1996-2016 is characterized by periods of both high and low annual rainfall totals (Figure 7). The year during which the initial study took place (1996) experienced above average rainfall while the two years immediately before the 2006 survey were either above average (2005) or average (2006) rainfall years. Although the total rainfall for 2016 is close to the 20 year average of 181 mm, nearly 60% of this amount fell in a single downpour in January 2016 during the warm summer period and long before the survey was undertaken in September. In 2016, only about 60 mm of rain fell in the study area over the period March-August and the region was considered to be experiencing drought conditions at the time of the survey in September 2016.

Table 4. Mean (\pm SE) number of adult shrubs sampled in 40 paired plots in commercial and communal rangelands over three periods. P-values show the level of significance following a t-test comparing the number of adult shrubs of each species in commercial and communal rangelands at each time step.

Species	1996			2006			2016		
	Commercial	Communal	p	Commercial	Communal	p	Commercial	Communal	p
<i>Galenia africana</i>	6.7 \pm 1.6	11.5 \pm 1.5	0.001	5.8 \pm 1.7	26.4 \pm 4.5	0.001	2.2 \pm 0.8	10.3 \pm 2.5	0.001
<i>Ruschia robusta</i>	78.0 \pm 10.0	51.6 \pm 11.8	0.02	73.7 \pm 8.4	56.6 \pm 12.3	NS	67.6 \pm 9.0	39.1 \pm 8.8	0.5
<i>Eriocephalus microcephalus</i>	13.8 \pm 2.9	6.0 \pm 1.6	0.001	21.0 \pm 4.4	8.9 \pm 2.6	0.001	18.4 \pm 4.1	7.2 \pm 2.9	0.2
<i>Tripteris sinuatum</i>	9 \pm 2.2	6.2 \pm 1.4	0.02	17.9 \pm 3.5	7.5 \pm 1.7	0.01	7.0 \pm 2.1	3.3 \pm 1.1	0.01
<i>Pentzia incana</i>	8.6 \pm 2.7	5.4 \pm 2.3	NS	16.9 \pm 5.9	11.2 \pm 4.2	NS	5.7 \pm 2.2	1.3 \pm 0.6	0.01

Table 5. Mean (\pm SE) number of seedlings of five shrub species in 40 paired plots on the commercial and communal rangeland in 1996 and 2016. P-values show the level of significance following a t-test comparing the number of seedlings in commercial and communal rangelands at the two time steps.

Species	No. seedlings					
	1996			2016		
	Commercial	Communal	p	Commercial	Communal	p
<i>Galenia africana</i>	2.7 \pm 0.7	5.6 \pm 1.6	0.001	0.4 \pm 0.3	19.3 \pm 9.2	0.001
<i>Ruschia robusta</i>	9.1 \pm 1.4	2.1 \pm 0.6	0.001	0.7 \pm 0.3	1.0 \pm 0.3	NS
<i>Eriocephalus microcephalus</i>	3.6 \pm 1.2	0.3 \pm 0.16	0.001	0.6 \pm 0.3	1.0 \pm 0.4	NS
<i>Tripteris sinuatum</i>	3.3 \pm 1	0.3 \pm 0.14	0.001	1.1 \pm 0.6	0.5 \pm 0.3	NS
<i>Pentzia incana</i>	0.4 \pm 0.2	0	NS	0.4 \pm 0.3	0.1 \pm 0.1	NS

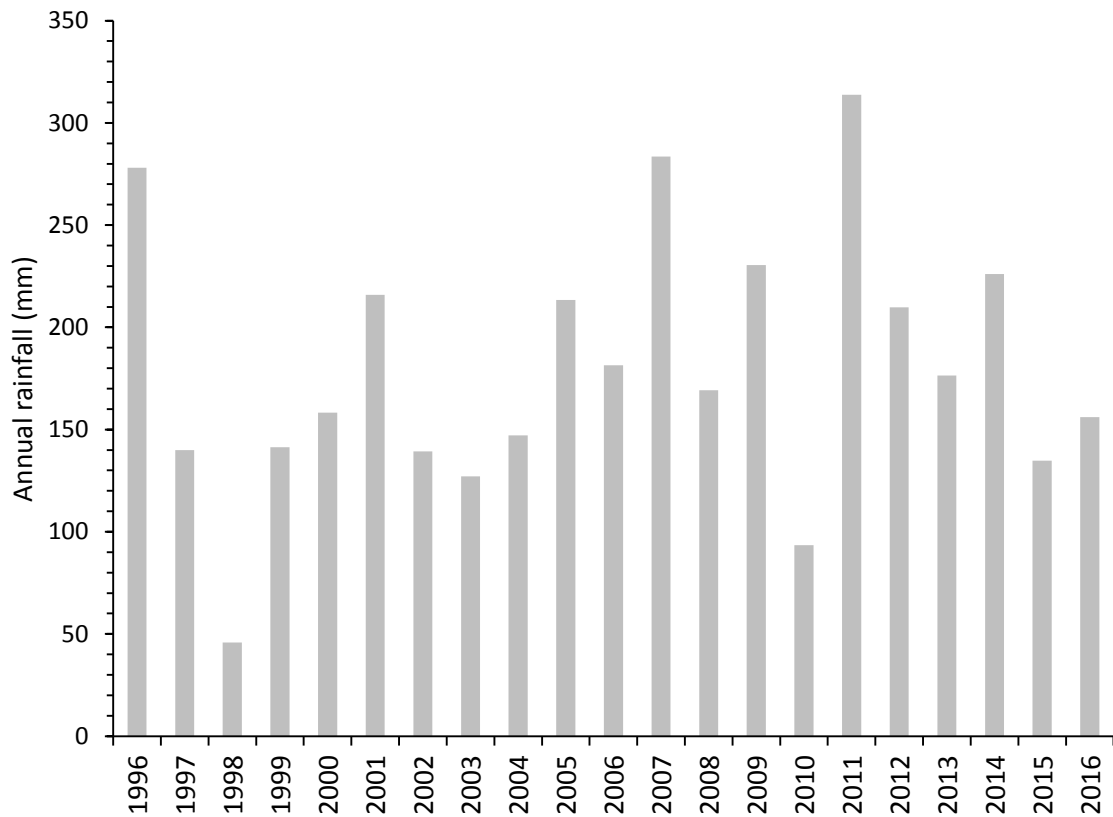


Figure 7. Annual rainfall totals (mm) for Paulshoek for the period 1996-2016. The mean annual rainfall for the time series was 181 mm.

Livestock

The number of goats and sheep in the communal area which were recorded at stock posts within two km of the sample plots has fluctuated considerably over the period 1998-2016 (Figure 7). Values for the periods 2003-04 and 2015-16 are especially low. However, the number of animals (97) utilizing the communal rangelands immediately before the 2006 survey was close to the maximum number (111) of animals recorded in 2008.



Figure 8. The number of sheep and goats per months within two km of the sample sites on the communal rangelands for the period 1998-2016.

DISCUSSION

Long-term changes (1996-2016) in cover, composition and species richness

Annuals are prominent in most arid and semi-arid regions including Namaqualand, where they contribute substantially to the productivity of these areas (Berg *et al.* 2012; Brown, 2002; Lane *et al.* 1998; Milton & Hoffman 1994). The cover of annuals also fluctuates over time and contributes to the variability in plant cover in Namaqualand. Rainfall has a significant effect on the cover and abundance of annuals since the amount of moisture affects seed germination, seedling growth as well as the survival of annuals (van Rooyen *et al.* 2015; Yan *et al.* 2015). Perennial plants are also influenced by rainfall and increase or decrease their biomass in response to available moisture (van Rooyen *et al.* 2015). The dry conditions experienced in the eight months immediately prior to when sampling was undertaken in 2016 contributed to the decline in both annual and perennial plant cover and therefore also to the decrease in total vegetation cover. In contrast, 1996 was an exceptionally high rainfall year and this is reflected in the high cover of annuals measured at the time. It is important to note the "lag phase" after the high rainfall season which is clearly evident in the graph. The high rainfall occurred in 2006, but the stock numbers only increased in the years after the high rainfall period, as the vegetation only established after the good rainy season due to the available soil moisture.

The total number of species recorded generally did not differ between commercial and communal plots although there were significant differences between years (Table 2 & Figure 4). Most of the variation between years was driven by changes in the number of annual species which were highest in 2006 and lowest in 2016. Since annuals are strongly dependent on rainfall these differences can be attributed to the rainfall totals which occurred in the period immediately prior to the surveys (Figure 7). The months just before the 1996 survey received above-average rainfall while for two years before the 2006 survey rainfall totals were above average or close to the average. In contrast, the months before the 2016 survey were dry and few annuals were present in either the commercial or communal plots during the survey period.

A pattern of high species richness on the communal side of the fence is consistent with that reported by Anderson and Hoffman (2007) for the lowland vegetation of the central

Namaqualand under sustained heavy grazing. It is also consistent with the trend for drylands in other parts of southern Africa (Rutherford *et al.* 2012; Hanke *et al.* 2014) and the world which generally exhibit an increase in annual plant cover in response to heavy grazing pressure. This is also facilitated by the large pool of annual species present in the Namaqualand, which are able to take advantage of the greater disturbance on communal rangelands and maintain high levels of species richness under high grazing pressure.

There is no evidence in the data set that any one of the growth forms has changed more in relative abundance or richness on either side of the fence over time. In other words, if a particular growth form (e.g. Succulent shrubs) had greater cover in commercial plots in 1996 then this pattern continued in subsequent surveys. Only rarely were values for individual growth forms in a treatment different between years (except for annuals which fluctuated considerably over time). As concluded by Todd & Hoffman (2009) differences between the two land tenure systems remained similar over the study period. There is little evidence for a relatively greater loss of cover over time in communal plots than commercial plots. However, neither is there evidence to suggest that a directional shift in growth form composition has occurred over the 20 year study period. The differences observed in 2016 were already well-established in 1996 and have not changed substantially since then. Paulshoek has been heavily grazed since the early 20th century (Rohde & Hoffman 2008) and fence lines were established from the 1950s onwards. This coincides with the period when communal areas became enclosed with clearly demarcated boundary fences in accordance with the apartheid policies enforced at the time.

Changes in the number and volume of key shrub species

Heavy grazing pressure on communal rangelands in the Succulent Karoo often results in an increase in the cover of unpalatable shrubs (Anderson & Hoffman 2007). It also causes a decline in the cover of palatable succulent and non-succulent perennial plants and in some cases a decrease in the diversity of perennial shrub species in an area as well (Milton 1995). Previous studies in the wider Leliefontein area have also shown that long-term continuous grazing has resulted in the replacement of palatable shrub species with unpalatable shrub species such as *Galenia africana* (Anderson & Hoffman 2007; Todd & Hoffman 2009). In general, the number of individuals of *Galenia africana* was higher in communal plots at all

time steps. In contrast, the number of individuals, and often the volume and size as well, for both palatable and highly palatable species, were higher in the relatively lightly-grazed commercial plots (Table 3). These patterns observed in the key species investigated in this study follow relatively predictable responses to grazing and disturbance. Such responses are well known and form the cornerstone of agricultural range management practices in semi-arid regions such as Namaqualand.

Changes in the number of seedlings and plant size class distributions

Recruitment patterns for the five key species studied showed predictable responses in reaction to differences in grazing pressure and rainfall. In 1996, the number of seedlings of *Galenia africana* was higher in communal plots while the number of seedlings of all other species was greater in commercial plots. Largely because of the general failure of rain in 2016 no seedlings were recorded on either side of the fence during the sampling period that year. The importance of rainfall for the recruitment and establishment of seedlings in Namaqualand has been shown elsewhere (e.g. Allsopp & Simons 2007). Riginos & Hoffman (2003) have also demonstrated the negative effect that heavy grazing has on the survival of palatable species in Namaqualand. Other studies have also shown the decline in seed set of succulent shrubs and particularly in communal rangelands, largely as a result of the heavy utilisation of flowers by sheep and goats (Milton 1995; Todd 2000; Carrick 2001).

Despite the low autumn and winter rain which characterises the period immediately prior to the 2016 survey, *Galenia africana* continued to have significantly more seedlings in communal plots. This suggests that seed production in this species is not affected by grazing while seed output of palatable shrubs is heavily impacted by herbivory. Seedlings and adult plants of *Galenia africana* are also generally poor competitors but thrive in the open conditions created by heavy grazing. They are also favoured by high impact disturbances such as are created by the trampling and the dunging of livestock. Individuals of this species often decline in volume as the cover of more competitive perennial shrubs increases.

An analysis of the size class distribution data for each of the five key species suggests that opportunity for growth and biomass accumulation appear to be relatively limited under the unpredictable and low rainfall conditions of the area. The large size discrepancies between treatments and years also suggest that palatable perennial species are being heavily utilised

by livestock, particularly in the communal areas. Many individuals of *Tripteris sinuatum* and *Pentzia incana* in particular are 'hedged' on the communal side of the fence in response to the heavy grazing treatment they receive on a regular basis. The palatable species in the communal plots were very small in 2016 relative to other years. This occurred primarily as a result of being heavily and selectively grazed as well as in response to the lack of rain in the period immediately prior to the 2016 survey. In contrast, the volume of *Galenia africana* doubled in the communal rangelands over the period 2006-2016. This was most likely as a result of the smaller individuals present in 2006 recruiting into the adult population class (Table 4, Figure 7).

Plant-herbivore dynamics and degradation of semi-arid rangelands

Continuous heavy grazing in the communal rangelands causes a decline in the quantity of perennial forage available for livestock. Instead, animals are more and more reliant on the availability of annual plants for their forage needs. The shift to an annual-dominated flora increases the variability in forage production which, in turn, increases the incidence of livestock mortality in the communal rangelands of Namaqualand (Todd & Hoffman, 1996; Rutherford & Powrie 2009; Riginos & Hoffman 2003; Vetter *et al.* 2012). Rainfall, however, has a strong influence on biomass production and forage quality in both grazing regimes and is the primary driver of plant composition in the area over extended time scales (Chollet *et al.* 2014). The number of animals also interacts with rainfall to influence the cover and composition of an area. This, in turn, influences the degree of degradation or change from an ungrazed condition (Vetter 2005; Campbell *et al.* 2005).

Results of this long-term study clearly show that the rainfall has an important influence on the differences between years while the stocking rate influences the differences between treatments. Similar findings were reported in South Australia where internal factors (e.g. herbivory) were found to be the prominent drivers of land degradation (Lawley *et al.* 2013). Heavy grazing causes a shift in plant community composition from palatable woody and succulent shrubs to ephemerals and unpalatable species. Although this shift does not result in a decline in overall species richness at the plot level, diversity at the landscape scale is maximised through a combination of heavily and lightly grazed areas. While there is a large pool of grazing-tolerant annuals present in Namaqualand there is also a pool of less grazing-

tolerant shrubs present which are likely to be lost from the landscape if there are no lightly grazed refuge areas present.

The shifts in the size of palatable species over time reflects natural shrinkage due to drought, but also removal of material by livestock. The larger size, and therefore biomass, of such shrubs on the commercial rangeland clearly provides a fodder bank that can be utilised in times of drought. On communal rangeland, however, the annuals which dominate the vegetation, do not form such pools for longer than a few months after the wet season. Therefore, they clearly do not have the same buffering capacity as the perennial shrubs. This dependency of the fodder supply on rainfall is indeed the hallmark of a non-equilibrium system (Westoby *et al.* 1989; Behnke & Scoones 1993; Wiegand & Milton 1996; Vetter 2005). Thus it can be conceived that the heavy grazing of the communal rangeland has shifted the system more towards one characterised by non-equilibrium dynamics. As such, it can be seen to be relatively resilient in its current state to the effects of livestock grazing and is not likely to degrade further. However, a consequence of this is that the variability in secondary production has also increased, which has implications for livelihoods.

Implications for policy and management

Livestock management has a strong influence on the vegetation dynamics of rangeland systems (Tiejen *et al.* 2007), and this is clearly also the case in the Namaqualand. Livestock in these communal areas utilize the vegetation within a 2 km radius from the same central stock post each day and as a result have a significant impact on the vegetation of the area (Riginos & Hoffman 2003). The decline in shrub biomass as a result of continuous grazing also has ecological and economic implications. The change in the species composition has also resulted in the decline in the primary productivity of the communal rangelands due to the change in the species composition by the displacement of the palatable shrub species with the unpalatable shrub species due to heavy grazing (O' Connor, 1991). This change has reduced the ability of the rangelands to withstand short-term increases in the forage demand. This, in turn, has increased the exposure of livestock to mortality during extreme weather conditions and periods of droughts (Riginos & Hoffman 2003; Todd & Hoffman 2009). Further decline will have an impact on those communities

who depend upon rangelands for their livelihoods. A decline in primary productivity inevitably also leads to poor quality livestock and lower market value (Tiejen *et al.* 2007).

The results of this study also have implications for the land-reform policy as local herders are in the process of expanding their livestock production enterprises. The findings from this study should be taken into an account when setting stocking rates for the new land reform farms. Setting new stocking rates was beyond the scope of the study but there is evidence which shows that high stocking rates, characteristic of communal rangelands will lead to significant changes in growth form composition over time. Failure to take this into account this will affect the diversity and composition of newly settled areas as well as the livelihoods of farmers in the long-term.

Opportunity for recovery may be possible although these are dependent on the ability of communal area farmers to move between different grazing areas on a regular basis. The effect of long-term, continuous heavy grazing on the vegetation of the Succulent Karoo is clearly demonstrated in the results of this study.

A long-term monitoring program which is adapted to local conditions should also be created, implemented and maintained over time to identify areas that are being continuously grazed. Such a monitoring programme should also record the mobility of different herds across the landscape over time. Encouraging herders to move on a regular basis will prevent the continuous grazing of an area causing further degradation of the vegetation. Such interventions may enhance the recruitment and survival of the palatable shrub species on the communal side of the fence. It will also increase the quantity and quality of the forage available for livestock particularly during drought periods.

CONCLUSIONS

This study compared long-term (1996 -2016) changes in plant species richness and growth form composition and cover in heavily grazed communal rangelands and lightly grazed commercial rangelands to determine if the patterns observed between 1996 and 2006 were consistent with those for the period 2006-2016. Results showed that there was a decline in the cover and species richness of some growth forms compared to previous years. This can be attributed primarily to the dry conditions experienced before the sampling took place in

2016. Drought had a disproportionate impact on annuals and geophytes relative to other growth forms. Although geophytes are perennials they function as annuals because they are only visible above ground for a short time each year and therefore behave in much the same way as annuals do.

This was especially apparent on the communal rangelands which are dominated by these growth forms. Such a decline in annual cover is to be expected in a landscape where the perennial cover has declined as a result of heavy grazing and which is now dominated by annuals. However, in terms of perennial plant cover the relative pattern of abundance between land use treatments was maintained across sampling periods. There is no suggestion in the data that the cover and species richness of perennial growth forms on communal rangelands are changing faster or more negatively than on the commercial rangelands.

The study also sought to examine the changes in five key shrub species (including palatable and unpalatable species) over 20 years, to determine whether they indicate further degradation of the communal rangeland or if they provide evidence of stability or recovery. Results showed that the abundance of key shrubs species was relatively stable over time. This indicates that, while there was some population turnover, an overall decline or increase has not occurred. However, there were significant changes in the volume of shrubs, indicating that grazing and drought both affect shrub volume. This suggests that palatable shrub species provide a fodder bank that can be utilised by livestock in times of drought. It appears that grazing is the mechanism that maintains the dominance of *Galenia africana* on communal rangelands, and if protected from grazing, palatable species are able to recover. Our findings suggest that further degradation is not occurring in the communal rangelands and very few significant changes have occurred since 1996 that cannot be explained by the drought conditions experienced in 2016.

In terms of arid and semi-arid rangeland dynamics the results suggest that at a low stocking rate the grazing system can be maintained at some equilibrium level where animal numbers remain constant while rangeland cover and composition also remains relatively constant. However, when a rangeland is grazed heavily for several decades, disequilibrium dynamics start to emerge. Under sustained, high grazing pressure, the vegetation changes from being dominated by perennials to annuals. Once this transformation has occurred, even relatively

low livestock densities would still maintain the dominance of annuals. This implies that recovery would take decades to occur even with complete removal of grazing. Given the short post-drought recovery periods that characterise most semi-arid systems, even low grazing levels may not lead to speedy recovery because edible forage is severely consumed and seed production and seed banks are not given the opportunity to recover. However, the frequency, timing and magnitude of rainfall events will also play an important role in vegetation recovery.

In terms of the implications for conservation and management it is important to note that continuous heavy grazing in spatially constrained grazing systems changes the vegetation from being perennial dominated (equilibrium) to annual dominated (disequilibrium). This switch to a disequilibrium system makes it more unpredictable in terms of forage and livestock production potential. This has important consequences for people's livelihoods. Vulnerable people who are not buffered from climatic, ecological and economic shocks will be most affected. For emerging farmers wanting to invest in commercial livestock production it is important to understand the role that perennial plants play in buffering forage supply especially in the low and unpredictable rainfall environments which characterise Namaqualand. Long term rainfall patterns also need to be considered.

REFERENCES

- Addinsoft 2017. Data analysis and statistics with MS Excel. Addinsoft, New York, USA.
- Adeel, Z. 2008. Findings of the Global Desertification Assessment by the Millennium Ecosystem Assessment: A perspective for better managing scientific knowledge. In: Lee C, Schaaf, T, editors. Future of Drylands. UNESCO; Paris: Pp. 677–685.
- Anderson, P.M.L. & Hoffman M.T. 2007. The impacts of sustained heavy grazing on plant diversity and composition in lowland and upland habitats across the Kamiesberg mountain range in the Succulent Karoo, South Africa. *Journal of Arid Environments* 70: 686–700.

- Asner, G.P., Archer, S., Hughes, R.F., Ansley, R J., Wessman., CA. 2004. Grazing systems, ecosystem responses and global change. *Annual Reviews of Environment Resources* 29: 261–99.
- Baker, L.E. & Hoffman, M.T. 2006. Managing variability: Herding strategies in communal rangelands of semi-arid Namaqualand, South Africa. *Human Ecology* 34: 765-84.
- Behnke, R.H. & Scoones, I. 1993. Rethinking range ecology: implications for range management in Africa. In: Behnke, R.H., Scoones, I., Kerven, C. (Eds.), *Range Ecology at Disequilibrium: New Models of Natural Variability and Pastoral Adaptation in African Savannas*. Overseas Development Institute, London (248 pp).
- Benjaminsen., T.A. Rohde., R.F., Sjaastad., E., Wisborg., P., Lebert., T. 2006. Land reform, range ecology, and carrying capacities in Namaqualand, South Africa. *Annals of the Association of American Geographers* 96: 224–240.
- Berg, N. & Steinberger, Y. 2012. The role of perennial plants in preserving annual plant complexity in a desert ecosystem. *Geoderma*: 185–186: 6–11.
- Boonzaier, E., Malherbe, C., Smith, A., Berens, P. 1996. (eds). *The Cape Herders*. David Philip Publishers, Claremont. 147 Pp.
- Bösing, B.M., Haarmeyer, D.H., Dengler, J., Ganzhorn, J.U., Schmiedel, U. 2014. Effects of livestock grazing and habitat characteristics on small mammal communities in the Knersvlakte, South Africa. *Journal of Arid Environments* 104: 124–131.
- Brown, G. 2002. Species richness, diversity and biomass production of desert annuals in an ungrazed *Rhanterium epapposum* community over three growth seasons in Kuwait. *Plant Ecology*. 165: 53–68.
- Campbell, B.M., Gordon, I.J., Luckert, M.K., Petheram, L., Vetter, S. 2006. In search of optimal stocking regimes in semi-arid grazing lands: One size does not fit all. *Ecological Economics* 60: 75–85.
- Carrick, P. 2001. Shrub community dynamics in a South African semi-desert. PhD thesis (unpublished). University of Cambridge, Cambridge. 245 Pp.

- Chesson, P., Gebauer, R. L.E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K., Weltzin, J.F. 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia* 141: 236–253.
- Chollet, S., Rambal, S., Fayolle, A., Hubert, D., Foulquié, D., Garnier, E. 2014. Combined effects of climate, resource availability, and plant traits on biomass produced in a Mediterranean rangeland. *Ecology* 95:737–748
- Cingolani, A.M., Noy-Meir, I., Di'az, S. 2005. Grazing effects on rangeland diversity: a synthesis of contemporary models. *Ecological Applications* 15: 757–773.
- Corder, G., Foreman, W., Dale I., 2009. Non-parametric statistics for non-statisticians. Hoboken: John Wiley & Sons. pp. 99–105. ISBN 9780470454619.
- Cornelissen, J.H., Lavorel, C.S., Gamier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden., M.G., Pausas, A.J.G., Poorter, H. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51:335.
- Cowling, R.M. & Hilton-Taylor, C. 1994. Patterns of plant diversity and endemism in southern Africa: an overview. In: Huntley, B. J. (ed.), Botanical diversity in southern Africa. National Botanical Institute, Pretoria. Pp. 31–52.
- Cowling, R.M., Rundel, P.W., Lamont, B.B, Arroyo, M.K, Arianoutsou, M. 1996. Plant diversity in Mediterranean climate regions. *Trends in Ecology and Evolution* 11: 362–366.
- Cowling, R., Rundel, P., Desmet, P., Esler, K. 1998. Extraordinary high regional-scale plant diversity in southern African arid lands: subcontinental and global comparisons. *Diversity & Distributions* 4: 27–36.
- Cuttelod, A., García, N., Malak, D.A., Temple, H. 2008. The Mediterranean: A biodiversity hotspot under threat. The 2008 Review of the IUCN Red List of Threatened Species. Intermediate Technology Publications, London (210 pp).
- Davis, F.W. & Goetz, S. 1990. Modelling vegetation pattern using digital terrain data. *Landscape Ecology* 4: 69–80.

- Deacon, H.J. 1992. Human settlement. Nutrients Fire and Diversity. In Cowling, R. M (eds): *The Ecology of Fynbos*. Oxford University Press, Cape Town. Pp. 260-270.
- Dean, W.R.J. & Milton, S.J. 2003. Did the flora match the fauna? Acocks and historical changes in Karoo biota. *South African Journal of Botany* 69: 68–78.
- Desmet, P.G. 2007. Namaqualand-A brief overview of the physical and floristic environment. *Journal of Arid Environments* 70: 570–587.
- Diaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D.G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H., Campbell, B.D. 2007. Plant trait responses to grazing: A global synthesis. *Global Change Biology* 13: 313–341.
- Dreber, N. & Esler, K.J. 2011. Spatiotemporal variation in soil seed banks under contrasting grazing regimes following low and high seasonal rainfall in arid Namibia. *Journal of Arid Environments* 75: 174–184.
- Driver, A., Desmet, P.G., Rouget, M. Cowling, R.M., Maze, K. 2003. Succulent Karoo Ecosystem Plan: Biodiversity Component Technical Report. CCU 1/03, Botanical Society of South Africa, Cape Town.
- FAO (Food and Agriculture Organization) 2004. *FAOSTAT Agriculture Data*. Food and Agriculture Organisation, Rome, Italy.
- FAO (Food and Agriculture Organisation) 2010. Land Degradation Assessment in Drylands (LADA). Assessing the status causes and impact of land degradation. LADA factsheet. Food and Agricultural Organisation, Rome, Italy.
- Haarmeyer, D.H., Schmiedel, U., Dengler, J., Bösing, B.M. 2010. How does grazing intensity affect different vegetation types in arid Succulent Karoo, South Africa? Implications for conservation management. *Biological Conservation* 143: 588–596.
- Hanke, W., Bohner, J., Dreber, N., Jurgens, N., Schmiedel, U., Wesuls, D., Dengler, J. 2014. The impact of livestock grazing on plant diversity in drylands: an analysis across dryland ecosystems and scales in Southern Africa. *Ecological Applications* 24: 1188–1203.

- Hendricks, H.H., Bond, W.J., Midgley, J. J., Novellie, P. A. 2005. Plant species richness and composition a long livestock grazing intensity gradients in a Namaqualand (South Africa) protected area. *Plant Ecology* 176: 19–33.
- Hobbs, N.T., Galvin, K.A., Stokes, C.J., Lockett, J.M., Ash, A.J., Boone, R.B., Reid, R.S. & Thornton, P.K. 2008. Fragmentation of rangelands: implications for humans, animals and landscapes. *Global Environmental Change* 18: 776–785.
- Hoffman, M.T. & Ashwell, A. 2001. Nature divided land degradation in South Africa. University of Cape Town Press, Cape Town, South Africa. 168 Pp.
- Hoffman, M.T. & Rohde, R.F. 2007. From pastoralism to tourism: The historical impact of changing land use practices in Namaqualand. *Journal of Arid Environments* 70: 641–658.
- Hoffman, M.T., Allsopp, N., Rohde, R.F. 2007. Sustainable land use in Namaqualand, South Africa: key issues in an interdisciplinary debate. *Journal of Arid Environments* 70: 561–569
- Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics* 22: 477-503
- Kelly, R.D. & Walker, B.H. 1976. The effects of different forms of land-use on the ecology of a semi-arid region in south-eastern Rhodesia. *Journal of Ecology*. 64: 553-576.
- Kuiper, S.M. & Meadows, M.E. 2002. Sustainability of livestock farming in the communal lands of southern Namibia. *Land Degradation and Development* 13: 1–15
- Lane, D.R., Coffin, D.P., Lauenroth, W.K. 1998. Effects of soil texture and precipitation on above-ground net primary productivity and vegetation structure across the Central Grassland region of the United States. *Journal of Vegetation Science* 9: 239–250.
- Milchunas, D.G., Forwood, J.R., Lauenroth, W.K. 1994. Productivity of long-term grazing treatments in response to seasonal precipitation. *Journal of Rangeland Management* 47:133–139.
- Milchunas, D.G., Sala, O.E., Lauenroth, W.K. 1988. A generalized model of grazing by large herbivores on grassland community structure. *American Naturalist* 132: 87-106.

- Milton, S.J. 1995. Spatial and temporal patterns in the emergence and survival of seedlings in arid Karoo shrubland. *Journal of Applied Ecology* 32: 145-156.
- Milton, S.J. & Hoffman, M.T. 1994. The application of state-and-transition models to rangeland research and management in arid succulent and semi-arid grassy Karoo, South Africa. *African Journal of Rangeland Forage Science* 11: 18–26
- Milton, S.J., Dean, W.R.J., du Plessis, M.A., Siegfried, W.R. 1994. A conceptual model of arid rangeland degradation. The escalating cost of declining productivity. *Bioscience* 44: 70–76.
- Mittermeier, R. A., Gil, P. R., Hoffman, T.M., Pilgrim, J., Brooks, T., Mittermeier, C. G., Lamoreux, J., da Fonseca, G. A. B. 2004. *Hotspots revisited*. Cemex, Mexico City, Mexico.
- Mucina, L., Jürgens, N., le Roux, A., Rutherford, M.C., Schmiedel, U., Esler, K.J., Powrie, L.W., Desmet, P.G., Milton, S.J. 2006. Succulent Karoo biome. In: Mucina, L., Rutherford, M. (Eds.), *The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia*, vol. 19. South African National Biodiversity Institute, Pretoria. Pp. 220-299.
- Naveh, Z. & Whittaker, R.H. 1979. Structural and floristic diversity of shrublands and woodlands in Northern Israel and other Mediterranean areas. *Vegetatio* 41: 171–190.
- Noy-Meir, I. & Oron, T. 2001. Effects of grazing on geophytes in Mediterranean vegetation. *Journal of Vegetation Science* 12:7 49–760.
- O'Connor, T.G. 1991. Local extinction in perennial grasslands: a life-history approach. *The American Naturalist* 137: 753–773.
- O'Connor, T.G., Haines, L.M., Snyman, H.A. 2001. Influence of precipitation and species composition on phytomass of a semi-arid African grassland. *Journal of Ecology* 89: 850–860.
- Olsvig-Whittaker, L.S., Hosten, P.E., Marcus, I., Shochat, E. 1993. Influence of grazing on sand field vegetation in the Negev Desert. *Journal of Arid Environments* 24: 81–93.
- Osem, Y., Perevolotsky, A., Kigel, J. 2002. Grazing effect on diversity of annual plant communities in a semi-arid rangeland: interactions with small scale spatial and temporal variation in primary productivity. *Journal of Ecology* 90: 936–946.

- Owen-Smith, N. & Danckwerts, J.E. 1997. *Herbivory. Vegetation of Southern Africa*. Cambridge University Press, Cambridge.
- Petersen, A., Young, E.M., Hoffman, M.T, Wynn-Jones, G.E., Musil, C.F. 2004. The impact of livestock grazing on landscape biophysical attributes in privately and communally managed rangelands in Namaqualand. *South African Journal of Botany* 70: 777–783.
- Phillips, D.L. & MacMahon, J.A. 1981. Competition and spacing patterns in desert shrubs. *Journal of Ecology* 69: 97–115.
- Riginos, C. & Hoffman, M.T. 2003. Changes in population biology of two succulent shrubs along a grazing gradient. *Journal of Applied Ecology* 40: 615–625.
- Rohde, R.F., Hoffman, M.T. 2008. One hundred years of separation: The historical ecology of a South African ‘Coloured Reserve’. *Africa* 78: 189-222.
- Rohde, R.F., Moleele, N.M., Mphale, M., Allsopp, N., Chanda, R., Hoffman, M.T., Magole, L., Young, E. 2006. Dynamics of grazing policy and practice: environmental and social impacts in three communal areas of Southern Africa. *Journal of Environmental Science and Policy* 9: 302–316.
- Rutherford, M.C & Powrie, L.W. 2009. Severely degraded dunes of the southern Kalahari: local extinction, persistence and natural re-establishment of plants. *African Journal of Ecology* 48: 930–938.
- Rutherford, M.C. & Powrie, L.W. 2010. Severely degraded rangeland: implications for plant diversity from a case study in Succulent Karoo. *South Africa Journal of Arid Environments* 74: 692–701.
- Rutherford, M.C., Powrie, L.W., Husted, L.B. 2012. Plant diversity consequences of a herbivore-driven biome switch from grassland to Nama-Karoo shrub steppe in South Africa. *Applied Vegetation Science* 15:14–25.
- Samuels, M.I., Allsopp, N., Hoffman, M.T. 2008. Mobility patterns of livestock keepers in semiarid communal rangelands of Namaqualand, South Africa. *Nomadic Peoples* 12: 123– 148.

- Samuels, M.I., Allsopp, N., Knight, R.S. 2007. Patterns of resource use by livestock during and after drought on the commons of Namaqualand, South Africa. *Journal of Arid Environments* 70: 728–739.
- Schmiedel, U., Röwer, I.U., Luther-Mosebach, J., Dengler, J., Oldeland, J.G. 2016. Effect of grazing on vegetation and soil of the heuweltjie veld in the Succulent Karoo, South Africa. *Acta Oecologica* 77: 27–36.
- Scoones, I. (Ed.) 1994, Living with Uncertainty. New Directions in Pastoral Development in Africa.
- Simons, L. & Allsopp, N. 2007. Rehabilitation of rangelands in Paulshoek, Namaqualand: Understanding vegetation change using biophysical manipulations. *Journal of Arid Environments* 70: 755–766.
- Tadey, M. 2006. Grazing without grasses: effects of introduced livestock on plant community composition in an arid environment in northern Patagonia. *Applied Vegetation Science* 9: 109–116.
- Tiejnen, B. & Jeltsch, F. 2007. Semi-arid grazing systems and climate change: A survey of present modelling potential and future needs. *Journal of Applied Ecology* 44: 425–434.
- Todd, S.W. 2000. Patterns of seed production and shrub association in two palatable Karoo shrub species under contrasting land use intensities. *African Journal of Range and Forage Science* 17: 22-26.
- Todd, S.W & Hoffman, M.T. 1999. A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. *Plant Ecology* 142: 169–178.
- Todd, S.W. & Hoffman, M.T. 2009. A fence line in time demonstrates grazing-induced vegetation shifts and dynamics in the semiarid Succulent Karoo. *Ecological Applications* 19: 1897–1908.
- van den Berg, J. A, 1983 . The relationship between the long-term average rainfall and the grazing capacity of natural veld in the dry areas of South Africa. *Proceedings of the Grassland Society of Southern Africa* 18: 165–167.

- van Rooyen, M.W., Le Roux, A., Geldenhuys, C., van Rooyen, N., Broodryk, N.L., van der Merwe, H. 2015. Long-term vegetation dynamics (40 years) in the Succulent Karoo, South Africa: Effects of rainfall and grazing. *Applied Vegetation Science* 18: 311–322.
- Vetter, S. 2005. Rangelands at equilibrium and non-equilibrium: recent developments in the debate. *Journal of Arid Environments* 62: 321–341.
- Vetter S. & Bond, W.J. 2012. Changing predictors of spatial and temporal variability in stocking rates in a severely degraded communal rangeland. *Land Degradation and Development* 23: 190–199.
- Watkinson, A.R. & Ormerod, S.J. 2001. Grasslands, grazing and biodiversity: editors' introduction. *Journal of Applied Ecology* 38: 233-237.
- Westoby, M., Walker, B.H., Noy-Meir, I. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42:266-274.
- Wiegand, T. & Milton, S.J. 1996. Vegetation change in semi-arid communities, simulating probabilities and time scales. *Vegetation* 125: 169-183
- Yan, H., Liang, C., Li Z, Liu, Z., Miao, B., He, C. 2015. Impact of Precipitation Patterns on Biomass and Species Richness of Annuals in a Dry Steppe. *PLoS ONE* 10(4): e0125300. doi: 10.1371/journal.pone.0125300.

APPENDIX 1. Expanded description of the five indicator species used in this study.

***Galenia africana* L. (AIZOACEAE)**

Galenia africana is a perennial, semi-deciduous woody shrub commonly known as Kraalbos because it is found abundantly at disturbed sites such as kraals (corrals). Individuals can grow up to 1 m in height. The small green leaves are grazed by livestock but turn yellow when they reach maturity or during the dry summer months. The dry leaves are believed to be toxic when ingested by livestock as they cause hepatic and cardiac changes in the physiology of sheep and goats. Excessive consumption of the leaves can cause a sickness referred to as water dropsy which can result in the death of animals (van der Vlugt *et al.* 1992). *G. africana* occurs in the western and southern parts of the Karoo and is primarily associated with the winter rainfall areas. It is an active invader species which occurs in association with disturbances such as heavy livestock grazing. It has become abundant in Paulshoek over the last 50 years in response to the heavy grazing pressure on the vegetation of the area from the start of the 20th century. Kraalbos grows in both sandy and rocky soils. It is spread over a wide area by animals due to the small size of the seeds which are ingested by sheep and goats and distributed in their dung. *G. africana* is also used by people for medicinal purposes to treat minor ailments such as toothache and dry scalp. It can also be applied as a paste to prevent tooth decay.

***Ruschia robusta* L. Bolus (AIZOACEAE)**

This 50-75 cm tall, perennial and evergreen, leaf succulent shrub is known locally by its Nama name, T'nouroeboos or more generally as one of the 'vygies' (little figs). It is widely distributed on rocky slopes and plains in the Northern Cape Province of South Africa (Raimondo & Cholo 2008). It is moderately palatable and is eaten by sheep, goats and donkeys. *Ruschia robusta* is common in areas which are grazed lightly but rarely survives in areas which are heavily overgrazed for long periods (Riginos and Hoffman 2003). The species can withstand long periods of drought and regenerates quickly after even low rainfall events. Like many leaf succulents in Namaqualand most of the root biomass is in the top 10 cm of the soil enabling them to absorb very low amounts of water and replenish

water supplies in their leaves. Carrick (2001) suggests that rainfall amounts as low as 6 mm can be utilised in this way. Branches are considerably thicker at the base of the plant and it is these parts of the stem that are utilized for fire (Solomon 2000). The species is covered in small purple flowers in spring which in turn produce hundreds of tiny seeds held in seed capsules which open during rain. The seeds are dispersed by the action of rain drops falling on the capsule. The abundance of *Ruschia robusta* has declined in Paulshoek particularly in the heavily-grazed sandy lowlands around stockposts and water points. *Ruschia robusta* appears not to be used for any medicinal purposes.

***Eriocephalus microcephalus* D.C. (ASTERACEAE)**

This evergreen, perennial shrub is known locally as Kapokbos (lit. 'Snow bush') or Wild Rosemary. While the species is endemic to South Africa it is widespread in the Northern Cape (Foden & Potter 2005). It possesses relatively strong, upright branches up to 75 cm in height with tiny aromatic leaves which are moderately palatable to livestock. The plant has small white bracts surrounding the flowers which contain distinctive orange anthers. Its most distinctive feature, however, is the woolly seeds which develop after flowering and remain on the plants for several months. This species is common in the landscape and is rarely grazed to local extinction. It can persist under even heavy grazing pressure. Perhaps because of the large number of seeds produced and their wide dispersal ability *E. microcephalus* recruits relatively easily in both disturbed and undisturbed rangelands. Next to *Galenia africana* is usually the most abundant perennial plant seedling observed at a site.

***Tripteris sinuatum* D.C. (ASTERACEAE)**

This species is a broad-leaved, drought-deciduous shrub with fleshy (rather than succulent) leaves. It is widespread in Namaqualand and across the Succulent Karoo biome and is amongst the most palatable species in the region (von Breda & Barnard 1991). Plants can grow to 50 cm if not grazed but on communal rangelands plants usually exist as small hedged individuals seldom taller than 15 cm in height. *T. sinuatum* produces showy yellows which are highly palatable to livestock. Because of this, individuals of this species seldom produce any seed in heavily-grazed rangelands. The seeds have wings, presumably to assist in their dispersal by wind. Following germination, plants can grow quickly and can flower in their first year if there is no competition from other plants or if they are not grazed first (van

Breda and Barnard 1991). This species is highly palatable to livestock and game and if not rested from heavy grazing will disappear from a local area.

***Pentzia incana* Thunb. (Kuntze) (ASTERACEAE)**

Pentzia incana is a low, perennial, semi-deciduous shrub commonly known as Skaapbossie (Sheep bush) or Ankerkaroo (Anchor Karoo) (von Staden 2012). The species is widely distributed across southern Africa and can be extremely common in the landscape, particularly in the more eastern parts of the Nama Karoo biome (Hobbs *et al.* 1975). Although it can grow up to 75 cm in height in moist habitats it is usually kept at 25 cm or less due to grazing. *P. incana* possesses an abundance of relatively thin, curved branches with small, aromatic leaves growing along the length of each branch. The leaves often dry out during the hot, dry summers of Namaqualand but can rehydrate easily again following even relatively small rainfall events. Branches sometimes curl over to touch the ground and in some parts of its distribution will regenerate vegetatively in this manner. The degree of palatability varies for this species but in the heavily-grazed communal areas of Namaqualand is considered one of the more palatable species present. *P. incana* is important for livestock but is also used medicinally to treat stomach ailments, toothache as well as bronchitis. Because of its aromatic properties it is also used as a spice on Karoo meat (Van Breda & Barnard 1991).

REFERENCES CITED IN APPENDIX 1

- Carrick, P. 2001. Shrub community dynamics in a South African semi-desert. PhD thesis (unpublished). University of Cambridge, Cambridge.
- Foden, W. & Potter, L. 2005. *Eriocephalus microcephalus* D.C. National Assessment: Red List of South African Plants version 2015.1. Accessed on 2017/03/10.
- Hobson, N.K., Jessop, J.P., Ginn, V.D.R., M.E., Kelly, J. 1975. Veld plants of southern Africa. Macmillan South Africa, Johannesburg.
- Raimondo, D. & Cholo, F. 2008. *Ruschia robusta* L.Bolus. National Assessment: Red List of South African Plants version 2015.1. Accessed on 2017/03/12

- Riginos, C., Hoffman MT (2003) Changes in population processes of two succulent shrubs along a grazing gradient. *Journal of Applied Ecology* 40: 615–625.
- Solomon, A.M. 2000. The sustainability of fuelwood utilization in Paulshoek, Namaqualand. MSc thesis (unpublished), University of Cape Town, Cape Town.
- van Breda, P.A.B., & Barnard, S.A. 1991. Veld plants of the winter rainfall region. Department of Agricultural Development. Pretoria.
- van den Berg, J.A. 1983. The relationship between the long-term average rainfall and the grazing capacity of natural veld in the dry areas of South Africa. *Proceedings of the Grassland Society of Southern Africa* 18: 165-167.
- van der Vlugt, J.J., Schultz, R.A., Fourie, N., Hon, L.J., Jordan, P., Labuschagne, L. 1992. *Galenia Africana* L. poisoning in sheep and goats: hepatic and cardiac changes. *Onderstepoort Journal of Veterinary Research* 59: 323-333.
- von Staden, L. 2012. *Pentzia incana* (Thunb.) Kuntze. National Assessment: Red List of South African Plants version 2015.1. Accessed on 2017/03/10.