Drivers of vegetation change in the eastern Karoo

by

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DEDICATION

For Dad

We all miss you so much. Thank you for teaching me so much, so early.

Christopher Ian Okes du Toit

1935-2017

PREFACE

The research contained in this thesis was completed by the candidate while based in the Discipline of Grassland, School of Life Sciences, of the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg Campus, South Africa. The research was financially supported by the Department Of Agriculture, Forestry and Fisheries.

The contents of this work have not been submitted in any form to another university and, except where the work of others is acknowledged in the text, the results reported are due to investigations by the candidate.

Signed: Kevin Kirkman, Supervisor

2019/09/03

Date

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Date: 30 August 2019

DECLARATION 2: PUBLICATIONS

My role in each paper and presentation is indicated. The * indicates corresponding author.

Chapter 2

du Toit JCO*, O'Connor TG. 2014. Changes in rainfall pattern in the eastern Karoo, South Africa, over the past 123 years. Water SA 40: 453–460.

The research reported on is based on data from the South African Weather Service and the Grootfontein Agricultural Development Institute. I collated and analysed the data and was lead author on the paper.

du Toit JCO, O'Connor TG. 2013. Apparent changes in rainfall pattern in the eastern Karoo, South Africa, over the past 123 years. Paper presentation to the Annual Congress of the Grassland Society of Southern Africa, 15th – 19th July 2013, Modimolle, South Africa. Presented by JCO du Toit.

du Toit JCO, O'Connor TG. 2013. Apparent changes in rainfall pattern in the eastern Karoo, South Africa, over the past 123 years. Paper presentation to the Arid Zone Ecology Forum, 2nd – 5th September 2013, Kimberley, South Africa. Presented by JCO du Toit.

Chapter 3

du Toit JCO*, Ramaswiela T, Pauw MJ, O'Connor TGO. 2018. Interactions of grazing and rainfall on vegetation at Grootfontein in the eastern Karoo. African Journal of Range & Forage Science 35: 267–276.

The research reported on is based on data from the Grootfontein Agricultural Development Institute (20th century data) and from a collaboration between the Grootfontein Agricultural Development Institute and the South African Environmental Observation Network (21st century data). I was part of the data collection team, analysed the data and was lead author on the paper.

du Toit JCO, Ramaswiela T, Pauw MJ, O'Connor TG. 2018. Rainfall/grazing interactions on vegetation composition at Grootfontein, JCO du Toit and TG O'Connor. Paper presentation to the Arid Zone Ecology Forum, 15th – 18th October 2018, Robertson, South Africa. Presented by JCO du Toit.

du Toit JCO, Ramaswiela T, Pauw MJ, O'Connor TG. 2018. Rainfall/grazing interactions on vegetation composition at Grootfontein, JCO du Toit and TG O'Connor. Paper presentation to the Annual Congress of the Grassland Society of Southern Africa, 23rd – 26th July 2018, Roodeplaat, South Africa. Presented by JCO du Toit.

Chapter 4

The research reported on is based on data from the Grootfontein Agricultural Development Institute (20th century data). I analysed the data and was lead author on the chapter. The chapter is currently being prepared for publication as a peer-reviewed article.

Chapter 5

du Toit JCO*, Nengwenani TP. 2016. Vegetation changes at the Boesmanskop Research Trials, Grootfontein, 2007-2015. Grootfontein Agric, 16: 21–32.

The research reported on is based on data from the Grootfontein Agricultural Development Institute. I was part of the data collection team, analysed the data and was lead author on the paper.

Chapter 6

du Toit JCO*, O'Connor TG. 2016. Minimum temperatures and frost at Grootfontein in the eastern Karoo, South Africa, over 98 years. Transactions of the Royal Society of South Africa 72: 39–46.

The research reported on is based on data from the South African Weather Service. I collated and analysed the data and was lead author on the paper.

Chapter 7

du Toit JCO*, van den Berg L, O'Connor TG. 2014. Fire effects on vegetation in a grassy dwarf shrubland at a site in the eastern Karoo, South Africa. African Journal of Range and Forage Science 32: 13–20.

The research reported on is based on data from the Grootfontein Agricultural Development Institute. I was part of the data collection team, analysed the data and was lead author on the paper.

du Toit JCO, van den Berg L, O'Connor TG. 2014. Fire, grass, and rainfall – the resilience of burnt veld in the eastern Karoo. Paper presentation to the Annual Congress of the Grassland Society of Southern Africa, 20th – 25th July 2014, Bloemfontein, South Africa. Presented by JCO du Toit.

Chapter 8

du Toit JCO*, O'Connor TG, van den Berg L. 2015. Photographic evidence of fire-induced shifts from dwarf-shrub-to grass-dominated vegetation in Nama-Karoo. South African Journal of Botany 101: 148–152.

The research reported on is based on data from the Grootfontein Agricultural Development Institute. I collected and analysed the data, and was lead author on the paper.

du Toit JCO, van den Berg L, O'Connor TG. 2015. Fire in the Nama-Karoo – a shift from dwarf-shrubland to sparse grassland. Paper presentation to the Annual Congress of the Grassland Society of Southern Africa, 20th – 23rd July 2015, Pietermaritzburg, South Africa. Presented by JCO du Toit.

Signed: Justin C.O. du Toit

Date: 30 August 2019

ABSTRACT

The Nama-Karoo Biome occupies much of the western central region of South Africa and transitions into the Grassland Biome along its eastern boundary along a gradual ecotone. The area is characterised by hot summers and long, frosty winters, relatively low rainfall, peaking in mid- to late-summer, with high inter-annual variability, and botanically by a co-existence of grasses and dwarf shrubs, with grass abundance positively related to average annual rainfall that increases from west to east. Biome shifts in response to changes in rainfall pattern and grazing have been suggested but never directly examined. Major drivers of botanical composition are rainfall and grazing by livestock. Fire is rare, occurring sporadically if high rainfall allows for good grass growth. This thesis focused on understanding the influence of rainfall, grazing, low temperatures, and fire on botanical composition at Grootfontein, a site in the ecotone between the Nama-Karoo and Grassland Biomes that is home to grazing trials up to 85 years old. The following specific questions were addressed:

Question 1: Over the long term, has Grootfontein shown patterns of rainfall cyclicity or experienced directional change, and how might these have influenced composition and productivity? Using data from 1888 to 2012, cyclicity in rainfall was evident for periods of approximately 20 and 60 years. Rainfall has also consistently increased since the mid-1970s, and this increase corresponds with a general pattern of increased grassiness in the eastern Karoo.

Question 2: How do rainfall and grazing, alone and in interaction, influence vegetation composition in the eastern Karoo? Compositional data from the 1960s and 2010s from various treatments at two sites at Grootfontein (Camp 6 and Seligman grazing trials) show a shift from dwarf-shrub- to grass-dominated vegetation, consistent with the increased rainfall over that time. An influence of grazing, both present and historical, was evident but secondary to the effect of rainfall. In some cases, there has been a shift to grassland. Data from the Camp 6 and Seligman grazing trials from the 1940s to the 1960s further indicate a combined influence of season of grazing and of rainfall. High-intensity summer-only grazing by livestock largely extirpates grasses and allows shrubs to thrive, while summer grazing in the form of rotational grazing or continuous grazing allow for a balance of grasses and dwarf-shrubs. Severe declines in both grasses and shrubs occurred apparently in response to drought, though the exact conditions required to cause such mortality remain unclear. Plant cover data from 2008 to 2015

from the Boesmanskop grazing trial showed that consecutive years of exceptionally high rainfall increased plant cover to nearly 100%, and increased the abundance of grasses. Competitive exclusion of dwarf-shrubs by grasses was not evident.

Question 3: What have been the trends in minimum temperatures, frost, and potential growth season at Grootfontein, how might these have influenced botanical composition and productivity, and is there evidence of increasing temperatures consistent with global warming? This is addressed using minimum-temperature data from 1916 to 2014. Minimum temperatures were lower than are usually reported. Variability in minimum temperatures was high, including a cooling from the 1910s to the 1950s and a warming from the 1950s to the 2010s. The length of the growing season (last frost to first frost of the subsequent season) varied considerably, and may have the potential to influence botanical composition.

Question 4: What is the influence of fire in Karoo vegetation? Based on the effects of a single fire on Grootfontein, fire killed some species while most species resprouted. Grasses appeared unaffected in terms of survival, several species of dwarf shrub (notably *Eriocephalus ericoides* and *Ruschia intricata*) were killed, and will need to re-establish by seed (termed nonsprouters), while most dwarf shrub species resprouted. This resprouter/ nonsprouter dichotomy was found to be evident at a range of other fire sites in the Karoo. Heavy grazing appeared to strongly impede the recovery of burnt veld, maintaining it as a sparse grassland dominated by annual species and occasional unpalatable shrubs. Should the grassiness of the Karoo continue to increase, then fire may become more frequent thereby maintaining a grassland state.

The findings allow for greater understanding of interactions among rainfall, grazing, and fire in eastern Karoo ecosystems, and these are discussed in the context of an existing state-and-transition model of eastern Karoo vegetation dynamics. The importance of long-term rainfall trends, rather than short-term variability, are highlighted. Long-term increases in rainfall will likely induce a biome shift to grassland, concomitant with a drastic reduction in dwarf-shrubs. This will likely alter both long-term carrying capacity for livestock and the type of animals that may be optimally stocked. Increased grassiness will result in the increased likelihood of fire, and if post-fire grass fuel loads remain above a critical level, a fire/grass feedback loop may be initiated whereby dwarf-shrubs are largely eliminated owing to their slow rates of growth or re-establishment. Introduction of infrequent fire will likely result in resprouter-dominated vegetation proliferating. It is demonstrated that the resilience of Karoo veld may be higher than previously thought, with severe grazing, droughts, and fire not pushing veld beyond a threshold into a state of denudation. Thus the prospects of conserving Karoo landscapes despite historical management remain high.

Some key future research efforts needed to improve our understanding of Karoo ecology include the life-histories of dwarf-shrubs, the conditions of drought and herbivory under which grasses and dwarf-shrubs die, and how and when perennial dwarf-shrubs and grasses regenerate. Based on historical trends, the continued existence of long-term research trials, such as those at Grootfontein, may be under threat and should receive attention.

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CHAPTER 1 INTRODUCTION

1.1 The Karoo and its biomes

The "Karoo" is a general term for an inland region of South Africa, bounded approximately by the towns of Steytlerville in the southeast and Robertson in the southwest, and along an arc in the north from Aliwal North, Kimberley, Upington, and through to Springbok in the west. The Karoo comprises several biomes, most characteristically the Nama-Karoo and the Succulent Karoo, but also Grassland, Azonal Vegetation, Albany Thicket, and Fynbos (Mucina and Rutherford, 2006). The largest of these is the Nama-Karoo Biome, and is the focus of the studies in this thesis.

The Nama-Karoo Biome occupies the inland western portion of South Africa and extends into Namibia (Mucina, Rutherford, *et al.*, 2006) (Figure 1.1). A key feature of the biome is that it is a shrubland (Moll and Gubb, 1989), usually dominated by dwarf shrubs but containing many other lifeforms including perennial and annual grasses, succulents, geophytes, herbaceous ephemerals, and occasional trees and larger shrubs. There is a general trend of increasing annual precipitation from west to east, corresponding loosely with the proportion of annual rain that falls during the summer months (Desmet and Cowling, 1999). Along this increasing rainfall gradient, there is an increase in the abundance of grass (notably perennial grasses) (Cowling and Roux, 1987), until the Nama-Karoo transitions into the Grassland Biome in the east. An exception is the Bushmanland region, where drought-tolerant *Stipagrostis* species flourish (Skinner, 1965). Nama-Karoo plants are primarily of the C_3 and C_4 photosynthetic types, with CAM plants comprising less than 10% of the total (Midgley and van der Heyden, 1999).

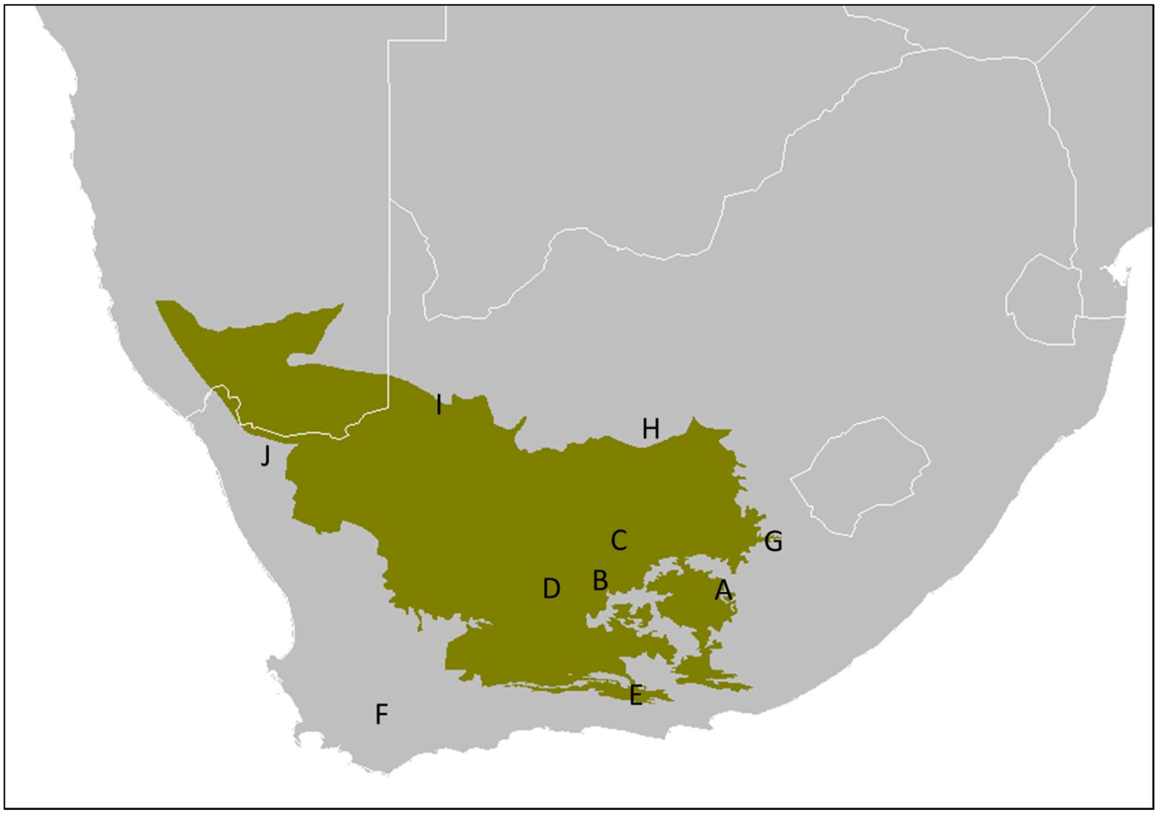


Figure 1.1 Location of the Nama-Karoo Biome (green) in southern Africa. (Image: Altatoron (2007)). Overlaid are the locations of towns mentioned in the text. A = Middelburg (Grootfontein), B = Richmond, C = De Aar, D = Victoria West, E = Steytlerville, F = Robertson, G = Aliwal North, H = Kimberley, I = Upington, J = Springbok.

1.2 Rainfall and vegetation in the Nama-Karoo

The Karoo has experienced major fluctuations in temperature in recent geological times (late Pleistocene and the Holocene), having been much cooler (5-6°C) about 20,000 years ago at the height of the last glacial era, which lasted until about 14,000 years ago. The current interglacial is about 10,000 years old, and experienced a hot, wet peak (about 2°C warmer) about 7,000 years ago. Such fluctuations would have influenced rainfall, though the nature of the relationship is not always clear (Meadows and Watkeys, 1999). There has therefore been considerable variation in rainfall, and this has influenced the relative proportions of Karroid dwarf shrubs and grass over the past few thousand years (Scott, 1989b; Scott and Lee-Thorp, 2004; Scott *et al.*, 2012), with summer rainfall being strongly correlated with grass cover (Bond *et al.*, 1994). An important implication here is that Karroid vegetation and its component species can survive fluctuations in rainfall, though presumably the geographical distribution and densities of species would change. In general, increased rainfall leads to increased grassiness, and *vice versa* (Acocks, 1953; Cowling and Roux, 1987). Accordingly, the relative proportion of grass and shrubs as determined by rainfall would mean that the position of the boundary between the Grassland and Nama-Karoo Biomes has shifted over time, with grassland 'moving' west in times of high rainfall, and east in times of low rainfall (Acocks, 1953; Mucina, Rutherford, *et al.*, 2006).

Recently, there has been a general shift toward increased grassiness in the Karoo, particularly in the eastern parts, the causes of which are uncertain, though it is recognised that increase in rainfall is likely to have contributed (Hoffman *et al.*, 1995). Rainfall in the eastern Karoo in recent decades has been higher than normal (du Toit, 2010), and these observations align with modelled predictions of increased rainfall for the region in the face of climate change: Engelbrecht *et al*. (2009) predicted a >10% increase in summer rainfall for the region approximately 60 km S and 20 km W of Middelburg in the SW and near Zastron in the NE.

The response of Karoo vegetation to rainfall has been described in both equilibrial and non-equilibrial terms. It has been argued that vegetation can attain an approximately stable 'climax' state (this is also agriculturally and ecologically desirable) that can be disrupted by heavy grazing and by droughts, after which it recovers (Vorster and Roux, 1983; Moll and Gubb, 1989). Alternatively, it has been proposed that Karroid vegetation shifts between different stable states in response, primarily, to rainfall and grazing (Milton and Hoffman, 1994). Both types of models, at least in terms of rainfall, may be true: Wiegand *et al.* (1995) demonstrated that depending on exactly how and when rain falls, both sudden, discontinuous changes as well as continuous and reversible changes in composition can occur. It remains uncertain how grazing would influence this. The relative importance of rainfall and grazing are also unclear, though timescales are probably important. Over the short-term, it is clear that rain induces a flush of short-lived species, while in the longer-term (several decades) the composition of perennial plants, notably grasses, is coupled to rainfall (O'Connor and Roux, 1995). Over shorter periods (approximately a decade), and if changes in rainfall are relatively small, then grazing may have a stronger effect. To this end, Roux and Theron (1987) note "Vegetation change brought about by domestic stock completely eclipses natural change". Milton *et al.* (2004), in their review of the dynamics of populations of perennial plants, concluded that while rain is of obvious importance, other factors may well play a role in recruitment and mortality. These include hail, frost, fire, and animal (including human) disturbances, the ingress of livestock in place of indigenous animals, alien plants, and modification of natural drainage patterns.

Droughts, a natural occurrence in semi-arid areas, were quickly recognised as a major constraint to livestock production and captured the attention of prominent citizens of the time: Olive Schreiner wrote of the drought of 1862 in her book Story of an African Farm:

> *"At last came the year of the great drought, the year of eighteen-sixty-two. From end to end of the land the earth cried for water. Man and beast turned their eyes to the pitiless sky, that like the roof of some brazen oven arched overhead. On the farm, day after day, month after month, the water in the dams fell lower and lower; the sheep died in the fields; the cattle, scarcely able to crawl, tottered as they moved from spot to spot in search of food. Week after week, month after month, the sun looked down from the cloudless sky, till the karoo-bushes were leafless sticks, broken into the earth, and the earth itself was naked and bare; and only the milk- bushes, like old hags, pointed their shrivelled fingers heavenward, praying for the rain that never came."* (Schreiner, 1883)

There is a cyclicity to rainfall in the Karoo, with one of the most prominent patterns being an approximately 20-year gap between droughts (Tyson and Dyer, 1978; Booysen and Rowswell, 1983). Severe droughts at the beginning of the 20th century prompted the formation of a commission of investigation into the problem, and culminated in the Final Report of the Drought Investigation Commission (du Toit *et al.*, 1923). Various recommendations were put forward, and the report also initiated the formation of various grazing trials at Grootfontein, findings from which transferred into the farming community as a whole and are in general still followed today. Despite judicious veld management, however, farmers generally are unable to protect themselves adequately from the effects of a severe drought (Myburgh, 1994).

It is thought that the presence of livestock during and immediately following a drought increases the incidence of mortality of perennial plants (Roux and Theron, 1987), and recommendations to remove animals from the veld for six weeks once the drought has been broken have been put forward (Anon, 1983). Animals still have to graze somewhere, but 'hardeveld' regions (stony areas with a good cover of low-nutritional value perennial grasses) should be selected for this. Sheep can feel the effects of drought more quickly than indigenous mammals (notably springbok) owing to their preference for grasses, but springbok may die in greater numbers as they may not opt to consume the supplementary feeds that sheep find readily acceptable (Davies and Skinner, 1986; Davies *et al.*, 1986).

1.3 Grazing and vegetation in the Nama-Karoo

Livestock have been present in the Karoo for probably at least 1800 years, when the Khoekhoen people kept Namaqua Afrikaner sheep (Snyman, 2014). However, it was only during European settlement that livestock numbers started increasing to approximately present-day levels, this trend having started as early as the mid- to late-1700s (Archer, 2000). Populations of indigenous herbivores were likely historically relatively low, although this relative absence was punctuated occasionally by huge herds of springbok in their search for food (Roche, 2004). The value of the Karoo as a hitherto unused resource for small-stock production was quickly identified (Andrew, 1889), as was the apparently detrimental effect that animals had on these semi-arid environments (Shaw, 1873). Degradation is usually seen as a decline in perennial grasses, a decline in palatable shrubs, an increase in unpalatable shrubs, an overall decline in cover, and an increase in erosion (Roux and Vorster, 1983b; Vorster and Roux, 1983; Archer, 2000; Arnalds and Archer, 2000). On the effect of sheep on Karoo veld, Brown (1875) noted:

> *"and it [topsoil erosion] is promoted, perhaps often induced, by the feet of the sheep ; they make little paths in every direction, and the water flows in these paths as so many little channels, washing away all the light earth, and then the grass roots get exposed and gradually disappear. Many farms which I remember fifteen or sixteen years ago to have been rich in grass are now almost bare of it, even in the most favourable seasons; and this process is, I believe, gradually but surely passing over the whole country, wherever sheep are introduced."*

The Final Report of the Drought Investigation Commission (du Toit *et al.*, 1923) highlighted how animals could degrade Karoo veld, and one of the key recommendations was that the system of kraaling (stockading animals at night in the same place) should be discontinued, and livestock should rather be confined to paddocks. This led to the system seen over most of the Karoo today, where animals stay in a paddock for several weeks to several months before being moved to the next, and without the need for night-time kraaling. However, did this lead to a reduced impact of animals on vegetation? Certainly it is likely that the discontinuation of kraaling would have eliminated the intense impact around kraaling sites, but what for the rest of the farm? Archer (2000) felt that maybe the opposite happened:

> *"New methods of watering and controlling livestock enabled a management strategy of higher stocking rates and more continuous grazing. This, in turn, accentuated biodiversity decline, visible as change in floristic composition, falling biomass, erosion of the soil and smaller seedbeds."*

In other words, 'judicious' veld management allowed greater numbers of livestock to be kept on Karoo veld, and what was needed to halt degradation was a reduction in the total number of animals. In part this reduction in livestock numbers came about by the development of guidelines on the carrying capacity of veld, and later a state-subsidised intervention, called the Stock Reduction Scheme, where farmers were paid to reduce the number of animals on their farms, particularly in the Karoo region (Hoffman and Todd, 1999). A condition of the Scheme was that farmers (who were not forced to participate) must reduce their stock numbers to two-thirds of that of the recommended carrying capacity. Thus, despite some farmers already having low stocking rates, the Scheme resulted in a considerably lowering of livestock numbers in the Karoo, especially considering that farmers generally stock at higher rates than those recommended (Danckwerts and Daines, 1981).

Following the recognition of the deleterious effects of livestock on Karoo vegetation, and the development of management approaches to minimise such effects, the next step was how to rehabilitate degraded veld, i.e. how to manage veld in such a way so as to return it to its 'pristine' condition. Early ideas were based on the premise of a basically equilibrial system (*sensu* Westoby, *et al*. (1989)), akin to the Range Condition Model proposed by Dyksterhuis (1949), where drought and heavy grazing degrade veld, and resting and high rainfall reverse this, although it was recognised that some types of degradation were irreversible (Roux and Theron, 1987), especially where topsoil had been lost (Archer, 2000). Empirical studies indicate that removal of livestock does not necessarily induce recovery, at least at the scale of several decades (Seymour *et al.*, 2010). Approaches to rehabilitate Nama-Karoo include judicious veld management (Roux and Vorster, 1983a) and various more intensive interventions, including soil disturbance, brush-packing, and re-seeding (Milton and Hoffman, 1994; Milton, 1995; van den Berg and Kellner, 2005; Dreber *et al.*, 2011), and high-intensity grazing by livestock (Beukes and Cowling, 2003).

Empirical studies of the influence of grazing on composition over time invariably recognise the importance of rainfall, which is sometimes interpreted as having a greater influence than grazing, and sometimes not (Roux and Vorster, 1983b; Hoffman, 1989; O'Connor and Roux, 1995). Therefore, when considering the influence of grazing on Karoo veld, the important influence of a highly variable rainfall environment must always be recognised. At Grootfontein, the interaction between drought and grazing was evident when a drought from 1948 to 1950, coupled with livestock grazing, caused the mortality of significant proportions of populations of grasses and, importantly, Karoo shrubs (Roux and Theron, 1987).

The effects of grazing have often been pronounced – after decades of study of Karoo ecosystems, Roux and Theron (1987) noted "*Vegetation change brought about by domestic stock completely eclipses natural change*". Here, 'natural change' presumably includes the influence of rainfall. Bond *et al.* (1994) concur, concluding from the results of carbon isotope composition ($\delta^{13}C$) of soil organic matter that grass cover has declined owing to grazing pressure by livestock. Smith (2000) demonstrates that grass cover in the central Nama-Karoo Biome has indeed decreased owing to grazing pressure by livestock, and shrub cover has increased independently of winter rainfall. Therefore, if livestock pressure controls grass and shrub populations (at least of palatable species), then it likely that competition between the two growth forms exerts a much smaller influence on abundance. Indeed, some shrub species may protect grasses from severe grazing owing to their thorny, inaccessible structure. Todd (2006), observing water-point induced grazing gradients, found that palatable species decline with heavy grazing, and that some unpalatable species increase. He went on to argue that grazing-tolerant species, such as the shrub *Pentzia incana* and the grass *Cynodon incompletus*, are very valuable for preventing system decline.

A key, repeated finding was that summer-only grazing was damaging to grass and many palatable shrubs, winter-only grazing protected most palatable plants, and some form of rotational grazing system that included season-long rests and excluded repeated seasonal grazing could protect palatable plants and optimise animal productivity (Gill, 1939; Tidmarsh, 1951; Roux *et al.*, 1981; O'Connor and Roux, 1995). Archer (2004) supported the idea of the importance of grazing strategies, finding that across different grazing systems vegetation cover differed even after rainfall had been accounted for.

1.4 Karoo vegetation and frost

Much if not all of the Nama-Karoo experiences sub-zero temperatures (i.e. frost) in winter (Mucina, Rutherford, *et al.*, 2006). In general, Karoo plants can survive frost even though they might be damaged to some extent (Donaldson, 1989). However, the growth rate of grasses (mainly C_4) is strongly hampered by low temperatures, while that of dwarf shrubs (mainly C_3) is reduced to a lesser extent (Vorster and Roux, 1983). Furthermore, plant growth is reliant on the availability of water. Therefore, under conditions of late rains and early frosts, the growth season of grasses may be very short (Mucina, Rutherford, *et al.*, 2006). This may have implications for the competitive interactions between grasses and shrubs, where late rains and early frosts would benefit shrubs, while summer rains and late frosts would benefit grasses.

1.5 Karoo vegetation and fire

During the 20th century the global importance of fire has been well described, and fire plays a crucial role in maintaining ecosystem functioning in many southern African vegetation types (Booysen and Tainton, 1984; Bond and Keeley, 2005). Before this, at least in South Africa, fire was long regarded as a damaging and unnecessary phenomenon, perhaps partly because of the damage it caused to livestock and human life, and to property, numerous examples of which are given by Brown (1877), who goes on to state:

> *"The miserable system of grass-burning, which neither legal enactment nor the voice of common sense appears to be able to prevent, is gradually denuding the country of herb, and sterility and barrenness must inevitably result from the continued destruction"*

When considering fire in the Karoo, it is important to recognise that eastern mountainous regions have been recognised as being grassland, at least since the 1950s (Acocks, 1953), while western mountainous regions were classified as Karoo or False Karoo. More recently, smaller hilly areas that used to be considered as part of the Karoo have now been re-classified as grassland (Mucina, Hoare, Lötter, *et al.*, 2006). Thus, the many reports (Downing *et al.*, 1978;

Booysen, 1984; Edwards, 1984) of fire in 'mountainous Karoo' or similar usually refer to fire in the Grassland Biome coterminous with the Nama-Karoo Biome.

Fire in the Karoo proper is rare owing mainly to a low combustible grass cover (Edwards, 1984; Cowling and Roux, 1987) and possibly a low density of lightning as an ignition source (Manry and Knight, 1986). However, during times of high rainfall, grass matter can accumulate to levels sufficient to support fire, such as in the mid-1970s when there was a much heightened incidence of fire in the Karoo (Huntley, 1984). It has been stated that if and when Karoo veld does burn, it is, or may be, highly damaging to vegetation (Booysen, 1984; Edwards, 1984; Cowling and Roux, 1987). Uncertainty shrouds such statements, as the authors acknowledge, owing to the absence of studies of this rare occurrence. One study that has since been cited in support of the statement is a report on the immediate effects of a fire near the Karoo Desert National Botanical Garden near Worcester in the Succulent Karoo Biome (Forrester, 1988). While being a valuable record, it gives no information on how plants recovered after being burnt. Trollope (1978) reports that fire kills or reduces the abundance of the unpalatable shrub *Chrysocoma tenuifolia* (now *C. ciliata*) where it encroaches into grasslands adjacent to the Karoo.

Thus the body of information on the effects of fire in the Nama-Karoo is tiny, despite it being recognised as a potentially important driver of change.

1.6 Study site: Grootfontein

Grootfontein is a research farm of approximately 10,000 ha and lies north of the town of Middelburg toward the eastern edge of the Nama-Karoo Biome (Mucina, Rutherford, *et al.*, 2006) where it interlaces with the Grassland Biome (Figure 1.2). Acocks (1953) originally classified the vegetation type as False Upper Karoo, reflecting the opinion that the vegetation of the area had become degraded through overstocking of livestock, allowing grasses to die out and Karroid shrubs to invade. In this classification, grass-covered hills were included as an integral component of the Karoo, but have since been recognised as being patches of the Grassland Biome. Most of Grootfontein is classified as Eastern Upper Karoo, Nama-Karoo Biome (Figure 1.3), though there are incidences of two grassland vegetation types on higher-lying ground, namely the Besemkaree Koppies Shrubland (Figure 1.4) and the Tarkastad Montane Shrubland (Mucina, Rutherford, *et al.*, 2006) (Figure 1.5).

Average seasonal rainfall is 370 mm per year (1916-2008), peaking in February (du Toit, 2010). Maximum rainfall intensity (2-year basis) is 20-25 mm per hour and 40-50 mm per day (Reich, 1961). Frost can occur from approximately mid-April to mid-October (du Toit, 1988).

At the Boesmanskop site at Grootfontein, generally considered to be in excellent condition and a 'benchmark' for the region, dominant dwarf shrub species are *Eriocephalus ericoides*, *Eriocephalus spinescens*, *Felicia muricata*, *Pentzia globosa*, *Pentzia incana*, and *Rosenia humilis*, dominant perennial grasses are *Cynodon incompletus*, *Digitaria eriantha*, *Eragrostis lehmanniana*, *Eragrostis curvula* subsp. *conferta*, *Sporobolus fimbriatus*, and *Themeda triandra*, and the most common short-lived grass species are *Aristida congesta* and *Chloris virgata* (du Toit and Nengwenani, 2013)

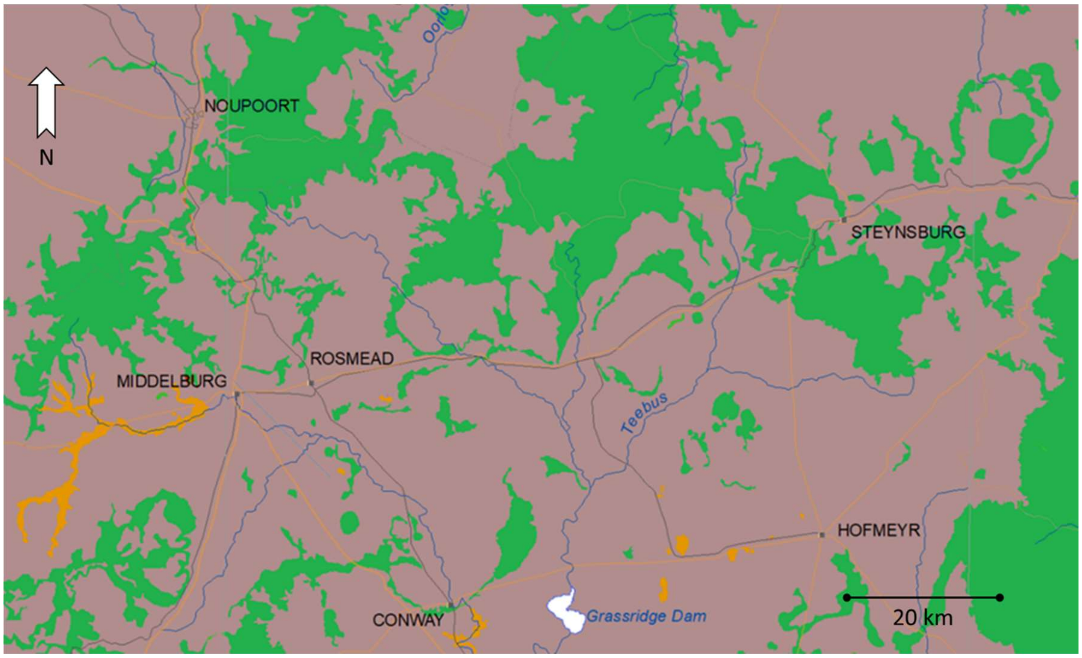


Figure 1.2. Vegetation types in the Middelburg district. Biomes are Nama-Karoo (light purple), Grassland (green) and Azonal (orange). White areas are water bodies, rivers are blue and roads are tan.

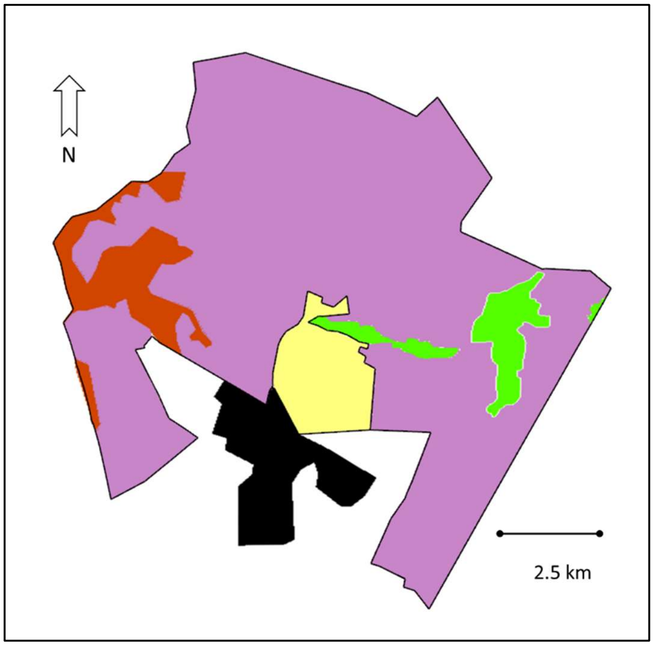


Figure 1.3. Vegetation types of Grootfontein include Eastern Upper Karoo (Nama-Karoo Biome; purple), Besemkaree Koppies Shrubland (Grassland Biome; red), and Tarkastad Montane Shrubland (Grassland Biome; green). Transformed land comprising cultivated pastures, lands, buildings, etc., is depicted in yellow. The farm lies to the west, north and east of the town of Middelburg (black polygon).

Figure 1.4. Example of the Eastern Upper Karoo vegetation at Grootfontein. Several species of perennial dwarf shrub, perennial grass, and annual grass are visible.

Figure 1.5. Example of Besemkaree Koppies Shrubland (Grassland Biome) at Grootfontein. Perennial grasses, the shrubs *Searsia* and *Diospyros*, and the succulent *Aloe broomii* are visible.

1.7 Summary and outline

The eastern Karoo ecotone has long shifted between Grassland and Nama-Karoo Biome states in response to rainfall, and the recent marked increase in grazing pressure following the introduction of livestock has advantaged the dwarf-shrub component at the expense of grasses. This region is characterised by high rainfall variation, some of which is cyclical, to which vegetation responds relatively quickly. A recent additional global driver is anthropomorphic climate change induced by increases in the atmospheric concentration of greenhouse gases, including CO_2 which also promotes plant growth and drought tolerance. Rainfall is predicted to become more erratic while possibly increasing, and this should act as a potent driver of vegetation change, possibly towards increased grassiness, but where droughts may cause widespread grass mortality. Livestock have had a reasonably well-documented general effect on Nama-Karoo vegetation, but a detailed conceptual model of the nature of these effects is lacking. It is of key importance to develop a more thorough understanding of how seasonality of grazing influences composition. Furthermore, the influence of livestock is likely to change in an increasingly grassy Karoo. Most importantly, management of Karoo agricultural environments for conservation and productivity will depend not on the individual effects of grazing and livestock, but on their interactive effects. Linked to this is that in the context of a warming world, small shifts in minimum temperatures and frost, coupled with changes in rainfall amount and seasonality, might have significant implications for the growth season on C_4 grasses (Sage and Kubien, 2003), perhaps to the point where grass/ dwarf shrub interactions are markedly changed. Added complexity to the balance of grasses and dwarf shrubs has been introduced in the form of fire, currently a rare dynamic but potentially of increasing importance should rainfall increase (Engelbrecht *et al.*, 2009), even in short spells, to provide the Karoo with sufficient fuel to support fire. A positive-feedback dynamic might thus emerge (Accatino *et al.*, 2010), where fire would promote grassiness because slow-growing shrubs would not have time to re-grow, and may also be at a competitive disadvantage (Smith, 2000).

In order to explore these issues, several overarching questions are posed and addressed in this thesis.

Question 1: What have been the patterns of rainfall cyclicity and directional change at Grootfontein, and how might these have influenced composition and productivity?

This question is addressed in Chapter 2 in a paper that presents the results of an examination of monthly rainfall data from 1888 to 2012 in the context of the findings of meteorological studies that report on rainfall in the Karoo.

Question 2: How do rainfall and grazing, alone and in interaction, influence vegetation composition in the eastern Karoo?

This question is addressed in three chapters. In Chapter 3, changes in botanical composition at several sites, from the 1960s to the 2010s, over which time there was a nett increase in rainfall, are examined. More specifically, three hypotheses relating to 1) the historical influence of heavy grazing, 2) whether grazing can maintain a dwarf shrubland despite increased rainfall, and 3) whether rainfall has induced a shift from Nama-Karoo to Grassland Biome are addressed.

In Chapter 4, data from the 1940s to the 1960s from two sites are examined to understand and characterise the influence of season of grazing, against a background of generally low rainfall and occasional droughts, on botanical composition with a focus on growth form. The general hypothesis that is addressed is that the higher the proportion of grazing that takes place in the summer, the greater the proportion of dwarf shrubs and the lower the proportion of grasses.

In Chapter 5, the influence of low rainfall years followed by high rainfall years on botanical composition and total cover, against a backdrop of lenient grazing, is examined.

Question 3: What have been the trends in minimum temperatures, frost, and potential growth season at Grootfontein, how might these have influenced botanical composition and productivity, and is there evidence of increasing temperatures as occur with global warming?

This question is addressed in Chapter 6 in a paper that presents the results of an examination of daily minimum temperature data from 1916 to 2014.

Question 4: What is the influence of fire in Karoo vegetation?

This question is addressed in two chapters. In Chapter 7, the influence of a single fire on a c. 20 ha piece of botanically diverse veld is examined, with a focus on whether individual species are killed by fire, i.e. are extirpated and whose recolonization would rely on seed, or can re-sprout after a fire.

In Chapter 8, a range of wildfires that occurred across the Karoo following several years of high rainfall were visited and photographed to test whether the predictions from Chapter 7 are generally applicable to Karroid vegetation, and what the additional influence of grazing has on general composition and structure.

Finally, in Appendix A, a series of photographs, referenced in the final discussion, are presented to offer the reader visual context of the work that is discussed in the thesis.

CHAPTER 2 CHANGES IN RAINFALL PATTERN IN THE EASTERN KAROO, SOUTH AFRICA, OVER THE PAST 123 YEARS

2.1 Introduction

Rainfall is a primary driver of the structure, composition and functioning of semi-arid vegetation communities (Gentry, 1988; Belsky, 1990; Anderson and Hoffman, 2007). In semi-arid rangelands rainfall amount may be highly variable over years and decades, although seasonal patterns (e.g. wet summers) may be relatively predictable. High rainfall variability can lead to droughts, which can significantly alter community composition through the die-off of plants (Westoby *et al.*, 1989). Extended periods, rather than single years, of above-average rainfall may induce significant ecological changes, such as the recruitment of woody plants (Kraaij and Ward, 2006), or increased grassiness leading to increased likelihood of fire (Scholes *et al.*, 2003). In the eastern Karoo, South Africa, vegetation composition is strongly related to rainfall amount and seasonality (Roux, 1966; Roux and Vorster, 1983b; Hoffman *et al.*, 1990; O'Connor and Roux, 1995). Rainfall amount in semi-arid regions increases plant growth, and rainfall seasonality is a potentially strong driver of vegetation composition in the eastern Karoo (Roux, 1966; Roux and Vorster, 1983b; O'Connor and Roux, 1995) because of the differential response of plant growth forms (importantly C_3 shrub and C_4 grass forms) to water availability across seasons (Epstein *et al.*, 1997). Similarly, rainfall concentration (how rainfall is distributed over the year) may control vegetation composition to some extent, as low-concentration rainfall (rainfall spread across much of the year) would presumably favour perennial plants that grow more or less continuously, while high-concentration rainfall (rainfall concentrated within a few months) would favour plants adapted to long periods of dry weather such as succulents, ephemerals, deciduous shrubs and dormant grasses. Therefore, changes in rainfall amount, seasonality, and concentration in the eastern Karoo would be expected to have a marked influence on vegetation and ecosystem functioning. Furthermore, understanding cyclical or directional changes in rainfall parameters, especially in the face of predicted increases in rainfall variability (Mason *et al.*, 1999) and amount (Hewitson and Crane, 2006), is necessary for understanding and managing this ecosystem.

In Africa, considerable research effort has been focused on identifying patterns in rainfall over time, and particularly cycles, at continental (Nicholson, 2000), regional (e.g. Tyson (1971) in South Africa), and local (e.g. Gertenbach (1980) in the Kruger National Park) scales. In South Africa a range of short-period cycles, in the order of 2–7 years, have been identified (Vines, 1980; Jury and Levey, 1993; Kane, 2009), although of greater interest has been a cycle with a period of approximately 20 years (Tyson, 1971; Dyer, 1975, 1976; Hall, 1976; Dyer and Tyson, 1977; Vines, 1980; Jury and Levey, 1993; Alexander *et al.*, 2007; Kane, 2009). Because data series are limited in length (usually <100 years), identifying cycles with a longer period is often impossible, although Kane (2009), using data from 1900 - 1998, did find evidence of 32–35 and 55–66 year cycles for parts of South Africa. Rainfall patterns have been linked to the Southern Oscillation Index (SOI) (Nicholson and Entekhabi, 1986; Kane, 2009), and the sunspot cycle (Dyer, 1976; Thresher, 2002; Alexander *et al.*, 2007), or a combination of the two (Stager *et al.*, 2007). Sunspots have been identified as having an 11-year cycle, while frequencies ranging from months to a few years (Nicholson and Entekhabi, 1986; An and Wang, 2000), 10–15 years (Sun and Yu, 2009), and 12–20 years (Torrence and Webster, 1999) have been found for the SOI. Additionally, the amplitude (variance of the signal) of the SOI signal varies at decade-level time scales (Gu and Philander, 1995).

The Grootfontein Agricultural Development Institute (Grootfontein hereafter) lies in the transition zone between the Nama-Karoo (dwarf shrubland) and Grassland Biomes in South Africa (Mucina, Rutherford, *et al.*, 2006). The boundary between the two biomes is determined mainly by rainfall amount, and possibly season (Rutherford and Westfall, 1986; Mucina, Rutherford, *et al.*, 2006). Therefore, vegetation might shift between Nama-Karoo and Grassland over time, depending on rainfall. A directional change would be anticipated to induce a single biome shift, while rainfall cyclicity might induce alternating biome states. Monthly rainfall data, including the occasional precipitation from snow, have been recorded at Grootfontein since 1888. This record provides a valuable resource for interpreting long-term rainfall, especially within the context of vegetation change which has been monitored on several long-term grazing trials at the site. Site-specific descriptions of rainfall are necessary for interpreting changes in vegetation at that site, considering the high variations in rainfall that can exist among even nearby locations (Kane, 2009).

The aim of this research was to describe ecologically relevant rainfall patterns that have occurred at Grootfontein from 1888 to 2011 in order to provide context for concomitant vegetation changes. We posed the following questions:

- Is there evidence of a directional trend or of cycles in (i) the amount of rainfall and (ii) the seasonality and concentration of rainfall, at Grootfontein?
- Are rainfall parameters correlated with the SOI?

2.2 Methods

2.2.1 Site description

Grootfontein, an agricultural research and training institute developed in 1911, lies in the Eastern Upper Karoo (Mucina, Rutherford, *et al.*, 2006). The vegetation is grassy dwarf shrubland dominated by annual and perennial C_4 grasses that grow primarily during summer, and mainly perennial C_3 shrubs that grow throughout the year (other than in mid-winter) depending on water availability.

Rain falls mainly during mid- to late-summer, with March usually recognised as the wettest month (Venter and Mebrhatu, 2005). Average annual rainfall is typical of a semi-arid summer rainfall area in South Africa; O'Connor and Roux (1995) report an annual average of 361 mm, with approximately 27% of the total falling during the cooler months of April to September. For the period 1916–2008, 68 of 86 years (79%) experienced rainfall of between 200 and 500 mm, and 58% of years had below-average rainfall (du Toit, 2010). In summer, days are warm to hot (30–35°C) and nights are moderately warm (10–16°C). Autumn days are warm (18–23°C) and nights are cool (6–10°C), with occasional light frosts occurring toward the end of the season. Winter days are moderate to warm (14–25°C) and nights are cold (−4–4°C) with frosts common. Temperatures as low as −10°C are usually experienced once or twice in winter. Spring days are warm to hot (28–31°C) and nights are cold to cool (2–8°C). Frosts usually continue until the middle of October. Light snow falls occasionally (absent most years), with heavier snowfalls having been recorded several times over the past century. Rainfall and temperature patterns combine to give four basic seasons: a very cold, dry winter, a warm, relatively dry spring, a hot and sometimes wet summer, and a warm and relatively dry autumn.

The year can also be divided into a warm season during which grass growth is favoured, and a cool season during which the growth of dwarf-shrubs is favoured (Roux and Vorster, 1983b).

2.2.2 Rainfall data set

Rainfall data for Grootfontein (31.4709° S, 25.0286° E) were derived from 3 sources, spatially all within several hundred meters of each other and therefore proximate enough to be treated as a single location. van Meerten (1927) provides monthly rainfall data from 1888–1926. The South African Meteorological Office provides daily rainfall data from 1916–1997 and from 2004–2008. Grootfontein provides monthly rainfall data from 1995–2012. Periods of overlap provide an opportunity to compare the similarity of the different sets of data on a monthly basis from 1916 to 1926, and 2004 to 2008. A paired t-test was conducted to compare monthly rainfall estimates from 2 sources. For 2004 to 2008, there was no difference between the estimates for the South African Meteorological Office (mean = 32.66, SD = 34.14) and for Grootfontein (mean = 34.03, SD = 33.56) records (t_{81}=-0.721, *p*=0.473). For 1916 to 1926, there was no difference between the estimates for the van Meerten (1927) data (mean = 28.95, SD = 34.93) and for South African Meteorological Office (mean = 28.44, SD = 34.24) records (t_{132}=-0.597, *p*=0.552). Owing to the similarity of the rainfall during the periods of overlap, an uninterrupted monthly rainfall record was constructed from 1888 to 2012 comprising data from van Meerten (1927) from 1888 to 1916, the South African Meteorological Office from 1917 to 1997, and Grootfontein from 1998 to 2012.

2.2.3 Data analysis

2.2.3.1 Rainfall seasons

Rainfall data were analysed at a range of resolutions comprising monthly, seasonal (four divisions (spring, summer, autumn, winter) and two divisions (warm, cool)), and annual (Table 2.1). Seasonal and annual periods were defined on account of their relation to plant growth.

Table 2.1. Aggregation of monthly data into seasons of various resolutions of rainfall data at Grootfontein. Within cells horizontal lines circumscribe when the seasons start and finish

Period	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
Spring[1]			|—	—	—|							
Summer[1]						|—	—	—	—|			
Autumn[1]										|—	—|	
Winter[1]	—	—|										|—
Cool[2]	—	—	—|						|—	—	—
Warm[2]				|—	—	—	—	—	—|			
Annual[3]	|—	—	—	—	—	—	—	—	—	—	—	—|

[1] Spring rainfall (September to November of Year t), Summer (December of Year t – March of Year $t+1$), Autumn (April to May of Year t), and Winter (June to August of Year t).

[2] Warm season rainfall (October of Year t to March of Year $t+1$) and Cool season rainfall (April to September of Year t).

[3] Annual rainfall (July of Year t to June of Year $t+1$; hereafter, a nominal year of, e.g., 1908, refers to rain from July 1908 to June 1909).

2.2.3.2 Patterns and trends in rainfall amount

To describe trends over time (increases and decreases within or across the data), time-series analysis using polynomial regression was conducted on original rainfall data, specifically for each of the months of September–April inclusive (May to August were excluded because of large numbers of zero values), all seasons (summer, autumn, winter, spring, cool, warm) and annual. First- to fourth-order polynomials ($a + bx + cx^2 + dx^3 + ex^4$, or subsets) were fitted to the data. Higher order models were excluded to avoid overfitting. If more than one model was significant ($p<0.05$), models were selected using the Akaike Information Criterion (AIC) values and F-tests. F-tests are appropriate because simpler models here are subsets of more complex models. Either a significant AIC test or a significant F-test warranted the acceptance of a model. Data were not transformed to achieve normality because (i) parametric comparisons were not being made, (ii) transformation would increase the likelihood of a Type 1 error, and (iii) transformation of data would likely result in a reduction of biological realism, because rainfall in semi-arid areas is approximately linearly related to primary plant production.

Unusually long runs of above- and below- average rainfall were calculated, where the probability (*P*) of an event (an above- or below-average year (*x*)) occurring sequentially a certain (*i*) number of times is given as:

$\overset{i}{P}_x = \left(\frac{n_x}{N_x}\right)^i$, where *n* is the number of events over at total of *N* years.

Therefore, the number of consecutive events relating to a certain value of *P* is:

$$i = \frac{\log_{10}(P_x)}{\log_{10}\left(\frac{n_x}{N_x}\right)}$$

Hence, the number of consecutive years of above- or below-average rainfall corresponding to a particular value of *P* can be calculated, and *P* values of 0.05 and 0.01 correspond to unusually long runs above or below the mean (1 run in 20 years, and 1 run in 100 years, respectively). The calculated value of *i*, usually having a decimal component, was rounded up to the nearest integer. This renders the actual *P*-value slightly lower than the nominal *P*-value. The number of consecutive years corresponding to the nominal *P* values was calculated for all seasons and months for above- and below-average rainfall.

2.2.3.3 Rainfall seasonality and concentration

The time of year at which rainfall peaks (assuming unimodal rainfall, as is the case at Grootfontein) is termed the seasonality. Rainfall usually peaks in mid- to late-summer at Grootfontein. Rainfall concentration is a measure of how rainfall is spread over the year: a concentration of 100% would mean that all rain fell in 1 month, and a concentration of 0% means that all months receive equal amounts of rain (Schulze, 1997). Rainfall season (Equation 2.1) and concentration (Equation 2.2) are calculated using the technique of Markham (1970), where rainfall amount has a magnitude (in mm), and each month has a direction (position on an arc; in degrees). Concentration values are expressed in terms of mean annual precipitation of the period in question (precipitation concentration index, Equation 2.3). Changes in seasonality and concentration over time were calculated using values derived from a 15-year running average.

$$\theta_t = \tan^{-1} \frac{\sum r_i \sin\theta_i}{\sum r_i \cos\theta_i}$$ Equation 2.1

$$r_t = \sqrt{\left(\sum r_i \cos\theta_i\right)^2 + \left(\sum r_i \sin\theta_i\right)^2}$$ Equation 2.2

$$P_c = r_t / MAP * 100$$ Equation 2.3

where: θ_t is the time of year (expressed as a direction, in degrees), r_i is the average monthly rainfall for month *i*, and θ_i is the month (expressed as a direction, in degrees), for each month, r_t is the rainfall concentration, P_c is the precipitation concentration index, and MAP is mean annual precipitation.

2.2.3.4 Rainfall periodicity

Spectral analysis is a method commonly used to reveal the temporal frequency at which single or multiple cycles within a time series occur (Dyer, 1975). Monthly and seasonal time series data, as well as annual SOI time series data, were smoothed using a binomial filter of the order 5 (Dyer, 1976). These were subjected to spectral analysis, for which 118 terms were used. Fisher's Kappa statistic was calculated to determine whether the series was simply 'white noise' or had some periodic component (Addinsoft, 2013).

Sine wave regression functions comprising 3 parameters (Equation 2.4) were fitted to rainfall and SOI data (annual and seasonal) filtered with a 10-year simple moving average and normalised to have a mean value of zero. The three parameters in the equation, *a*, *b*, and *c*, reflect amplitude (height of a peak), period (distance between peaks), and shift (position of the wave along the *x*-axis) of the wave function. Regressions were accepted as statistically significant if the overall model and each of the three coefficients had a $p<0.05$.

Where spectral analysis provided evidence of multiple cycles, a more complex double-wave cosine function (Equation 2.5) was fitted to the data to explore whether the data showed evidence of two overlaid cycles (Dyer, 1976). More complex models were accepted based on AIC values.

$$y = a\sin\left(\frac{2\pi x}{b} + c\right) \qquad \text{Equation 2.4}$$

$$y = a + b\cos\left(\frac{2\pi x}{c} + d\right) + e\cos\left(\frac{2\pi x}{f} + g\right) \qquad \text{Equation 2.5}$$

2.3 Results and Discussion

2.3.1 Rainfall seasons

Average annual rainfall was 372 mm with a wide range, typical of semi-arid areas, from 118 (in 1907) to 731 mm (in 1890) (Figure 2.1). Average cool season rainfall (93 mm) is approximately one third that of the average warm season rainfall (278 mm) and one quarter of the mean annual rainfall. Fifty-eight percent (58%) of the total annual rainfall falls in summer, with the next wettest season being spring. Winter rainfall is approximately 10 mm per month. For all seasons and all months the mean rainfall is higher than the median, reflecting the typical positive skewness of rainfall data in semi-arid regions.

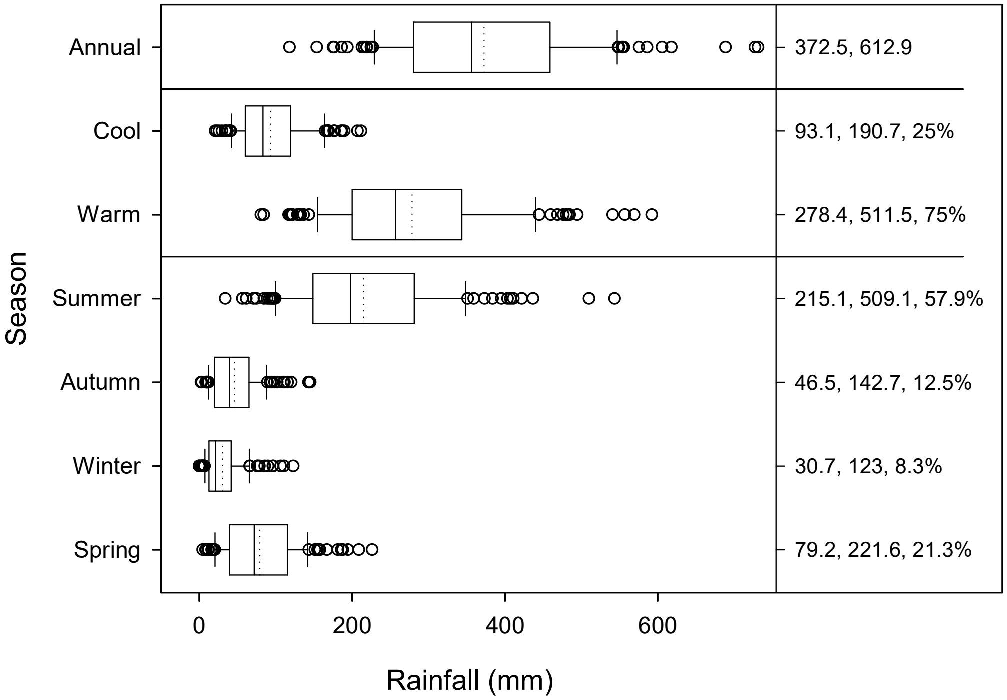


Figure 2.1. Box and whisker plot of annual rainfall at Grootfontein using 3 resolutions. Boxes bound the 25th and 75th percentiles and show the median (solid line) and mean (dotted line). Whisker bars bound the 10th and 90th percentiles, and outliers are shown as dots. Comma-separated numbers are the mean, range, and per cent contribution to the total average rainfall, respectively.

2.3.2 Rainfall amount

Significant trends over time, explaining between 13 and 19% of the variation, were evident for January, 'summer', 'warm season', and 'annual' (Figure 2.2). In all cases 4th order polynomial models best described the trends (Table 2.2). The most general pattern that emerges is a ‘W’ shape, where rainfall was high during the late 1800s (annual average = 459 mm from 1889 to 1898), low for the first third of the century (annual average of 319 mm from 1899-1937), rose slightly in the middle of the century (annual average of 401 mm from 1938–1952), dipped until the mid-1980s (annual average of 353 mm from 1953–1984), and rose again until present day (annual average of 426 mm from 1985–2010) (Figure 2.2). The month of January appears to be important in determining wet years, and this in turn contributes to high totals for 'summer', 'warm', and 'annual' seasons. Of the 20 highest totals for January, 14 (70%) occurred either during the 1890s or since 1985.

Notably, linear regression analysis ($y=ax+b$) revealed that there were no significant directional trends (although all were positive) for any months or seasons or for annual rainfall over time (all $p>0.08$), consistent with Kane (2009). If dealing with shorter datasets, e.g. 1888-1973, or 1950-2015, then significant trends would be seen. While these would certainly influence botanical composition and ecosystem functioning, extrapolation of either of those regressions would give false predictions. This highlights the importance of recognising the time horizon needed to assess possible climate change impacts on rainfall, and the need for long-term data sets.

Table 2.2 Regression and test statistics of polynomial distributions fitted to months September–April, all seasons, and to annual rainfall data at Grootfontein. Only significant regressions are presented.

Model parameters ($y=a + bx + cx^2 + dx^3 + ex^4$)									Comparison with next best model (based on AICC)			
Data	*a*	*B*	*c*	*d*	*e*	F ratio	*P*	R^2	Δ AICC	*P* (AICC)	F ratio	*P* (F ratio)
Jan	104.4	−6.927	0.2187	-2.600×10^{-3}	1.049×10^{-5}	5.38	<0.001	0.155	4.54	0.09	4.36	0.015
Summer	307.4	−13.00	0.4250	-5.220×10^{-3}	2.150×10^{-5}	4.62	0.002	0.136	3.12	0.17	3.64	0.03
Warm	411.4	−17.87	0.5665	-6.702×10^{-3}	2.681×10^{-5}	5.30	<0.001	0.125	5.17	0.07	4.69	0.01
Annual	543.8	−23.78	0.773	-2.600×10^{-3}	2.150×10^{-5}	6.71	<0.001	0.187	10.45	0.01	7.49	<0.001

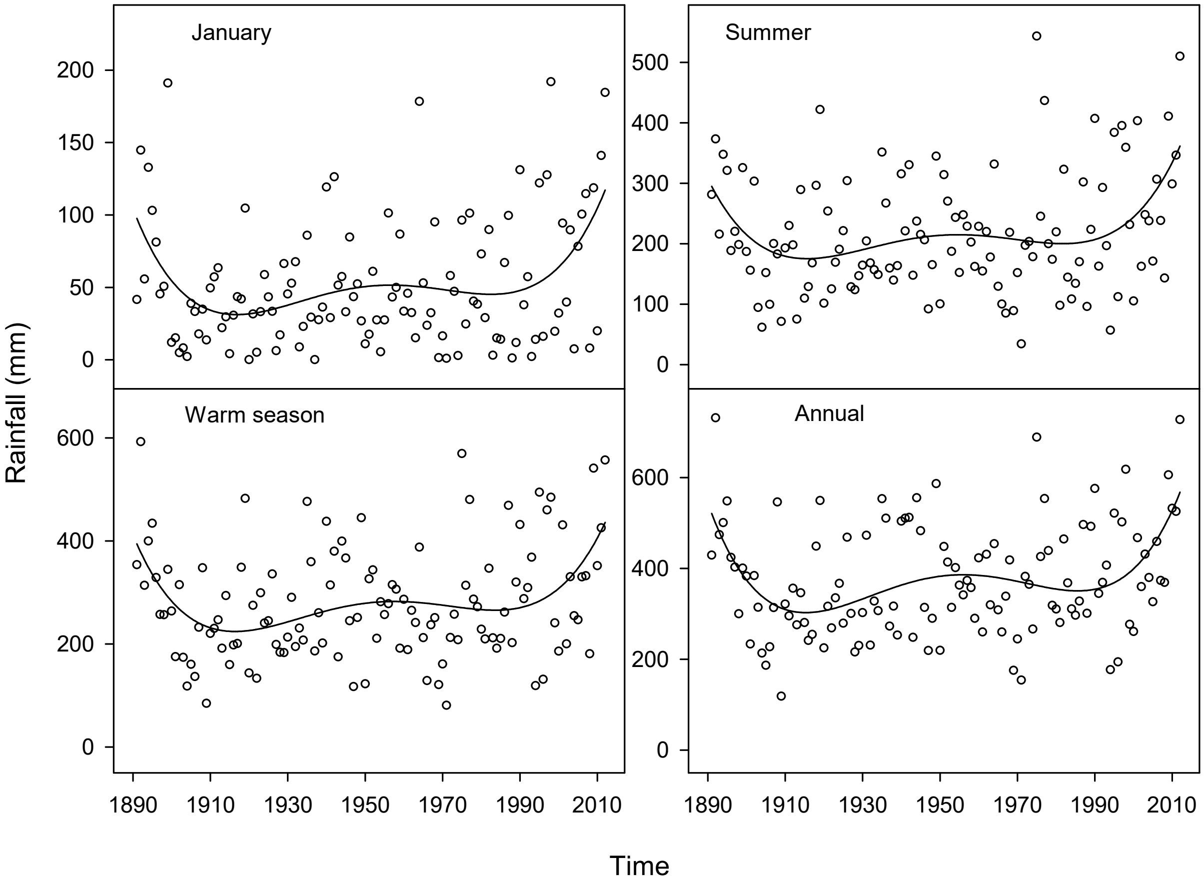


Figure 2.2. The four time periods that exhibited significant trends over time in rainfall at Grootfontein. Lines are 4th-order polynomial regressions (see Table 2.2 for details).

Unusually long above- or below-average runs were found for all seasons and all months (Figure 2.3). The high rainfall of the end of the 19th century is clearly evident during summer (January), autumn (March–May), and winter (June). The high rainfall of the late 1800s reflects good rains over much of the country at that time (Tyson and Dyer, 1975). There were scattered above-average runs during the 1970s, generally considered to be a wet decade, while the high 21st century rainfall is associated with above-average 'summer' runs, but not with individual months.

A near-continuous run of below-average years from 1907 to 1923 reflects the droughts that occurred during that period, which at the time prompted an in-depth investigation by the South African Government (du Toit *et al.*, 1923). Before the respite of the mid-century, further below-average 'summer' and 'autumn' runs, associated with particularly dry Octobers and

Februarys, took place from 1925 to 1934. The 1960s was in general a dry decade, with long runs of low-rainfall, 'warm', 'spring', and 'summer' seasons (see also Tyson and Dyer, 1978). While the 1980s are well recognised as a decade of drought (e.g. Nicholson, 1989), there were few long runs of dry years, probably owing to interjections of high rainfall events such as Cyclone Domoina (Mason *et al.*, 1999).

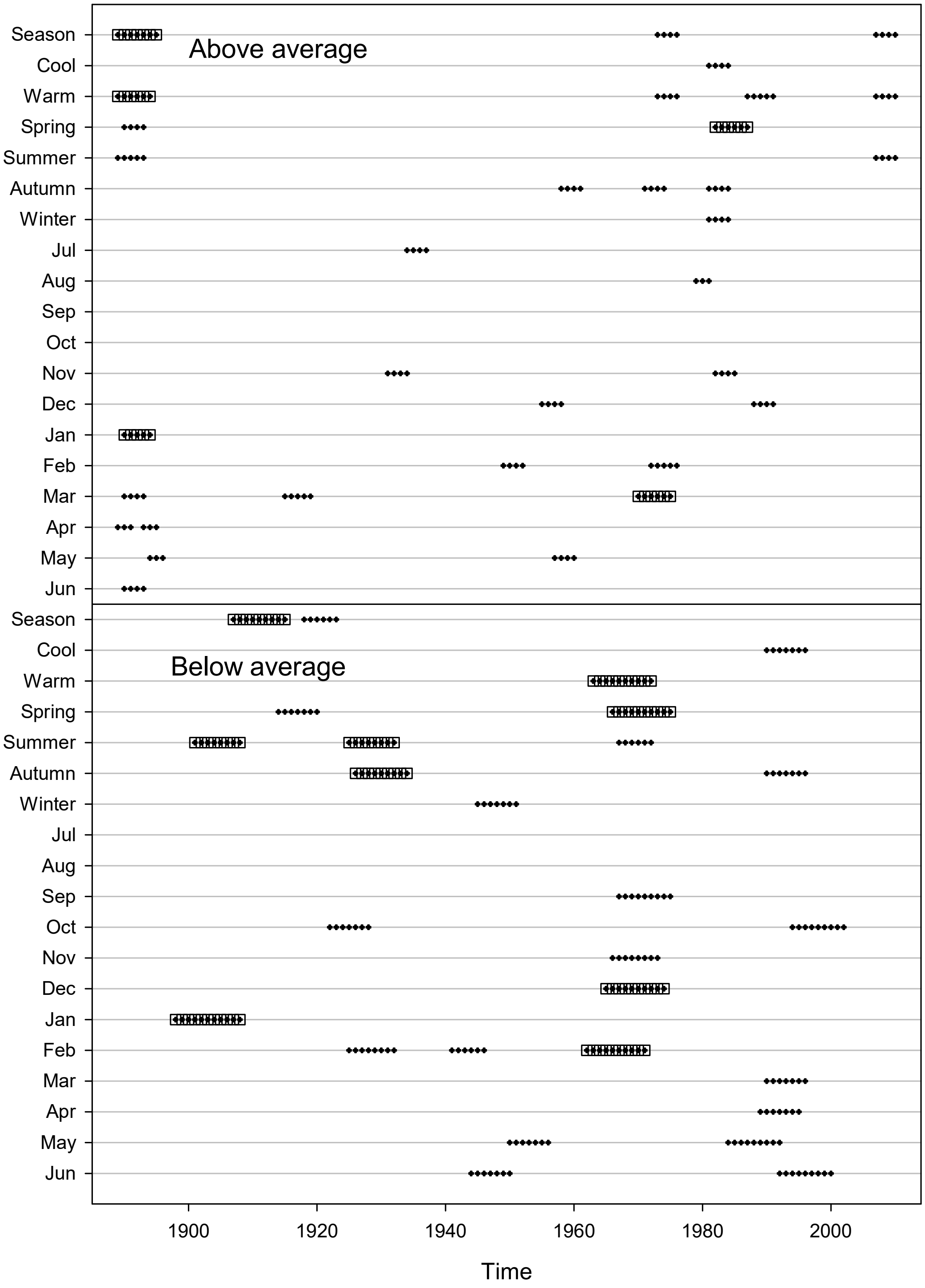


Figure 2.3. Unexpectedly long above- or below-average runs for seasons and months at Grootfontein. Boxes are $p<0.01$ (1 in 100 years) and plusses are $p<0.05$ (1 in 20 years). See text for details.

Spectral analysis identified the frequencies of cycles for various seasons and SOI (Figure 2.4). For 'spring', 'autumn', 'winter', 'warm', 'cool', and 'annual' seasons, the strongest signal was somewhere between 40 and 60 years, which is consistent with findings of Kane (2009). For 'summer', the strongest signal was around 20 years, consistent with the findings of various authors (Tyson, 1971; Jury and Levey, 1993; Kane, 2009), with a secondary signal at 60 years. The SOI data also showed a signal at around 60 years, with other signals at about 13 and 9 years.

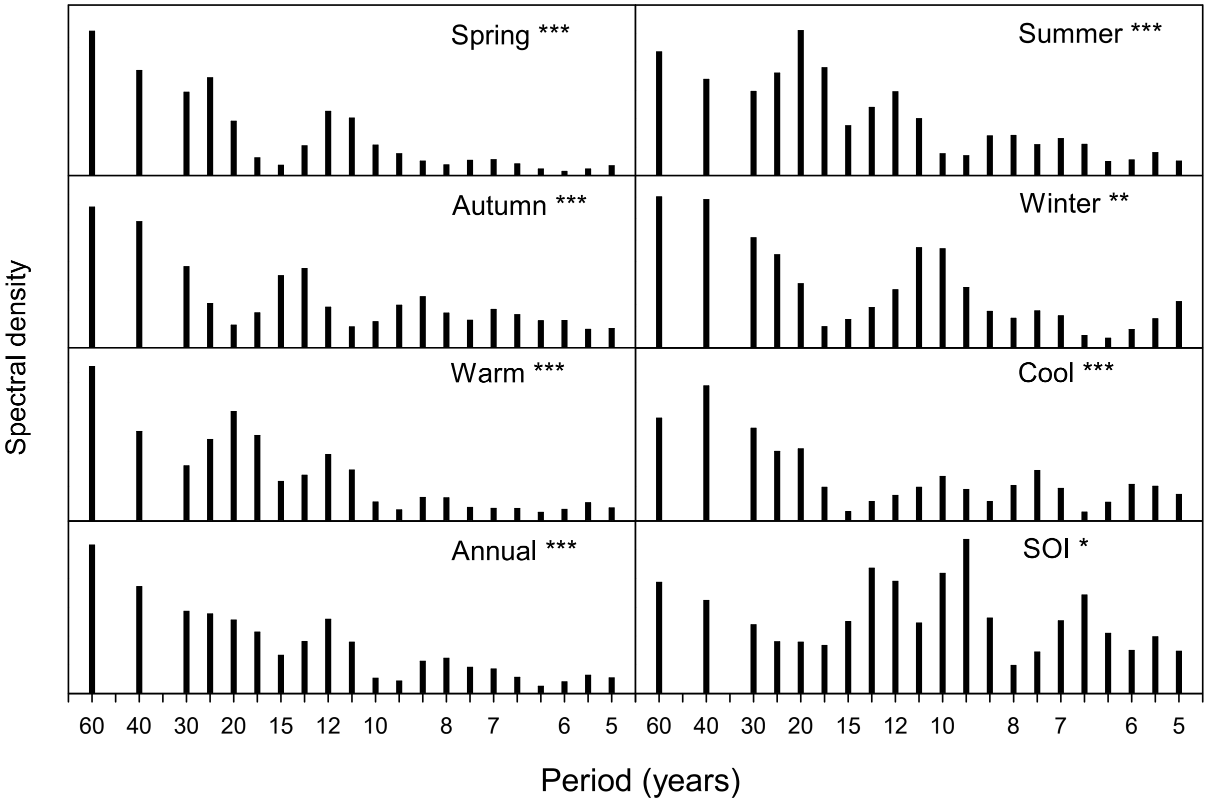


Figure 2.4. Variance spectra for climate parameters (rainfall and SOI). Superscripts reflect the probability of the time series being ‘white noise’, as estimated by Fisher’s Kappa statistic (ns: $p>0.05$; *: $0.01<p\leq0.05$; **: $0.001<p\leq0.01$; ***: $p\leq0.001$).

Rainfall cycles were apparent in annual rainfall and during all individual seasonal classes, and for the SOI (Figure 2.5). For all seasons other than spring, a double-wave cosine model provided a better fit, and was statistically more acceptable based on AIC values (for all models $p<0.001$). In all cases, the shorter cycle lay between 18 and 24 years, consistent with the approximately 20-year cycle found by others. The longer cycle ranged from 44 to 77 years, which is in general agreement with Kane (2009). These findings are consistent with the prediction of Dyer (1975) that several interacting cycles may influence southern African rainfall. Evidence of a long-term cycle of 44 years was suspected by Dyer (1975) for winter rainfall in South Africa, although that data record was too short to be certain. His 44-year cycle may correlate with the winter rainfall (43.5 years) cycle of this study.

This record is 123 years which allows the longer cycle to be identified, but its magnitude remains unclear. For example, for annual rainfall a short-term cycle of 21.7 years and a long-term cycle ranging from 45 to 80 years (the approximate range of long-term cycles found over all seasons) provide statistically significant ($p<0.02$) fits to the data (Figure 2.6). This indicates that a long-term cycle, in the order of 45–80 years, may be common to all seasons, and this correlates to similar fluctuations in the SOI. Long-term correlations between rainfall and SOI have been found elsewhere (e.g. Nicholson and Entekhabi, 1986).

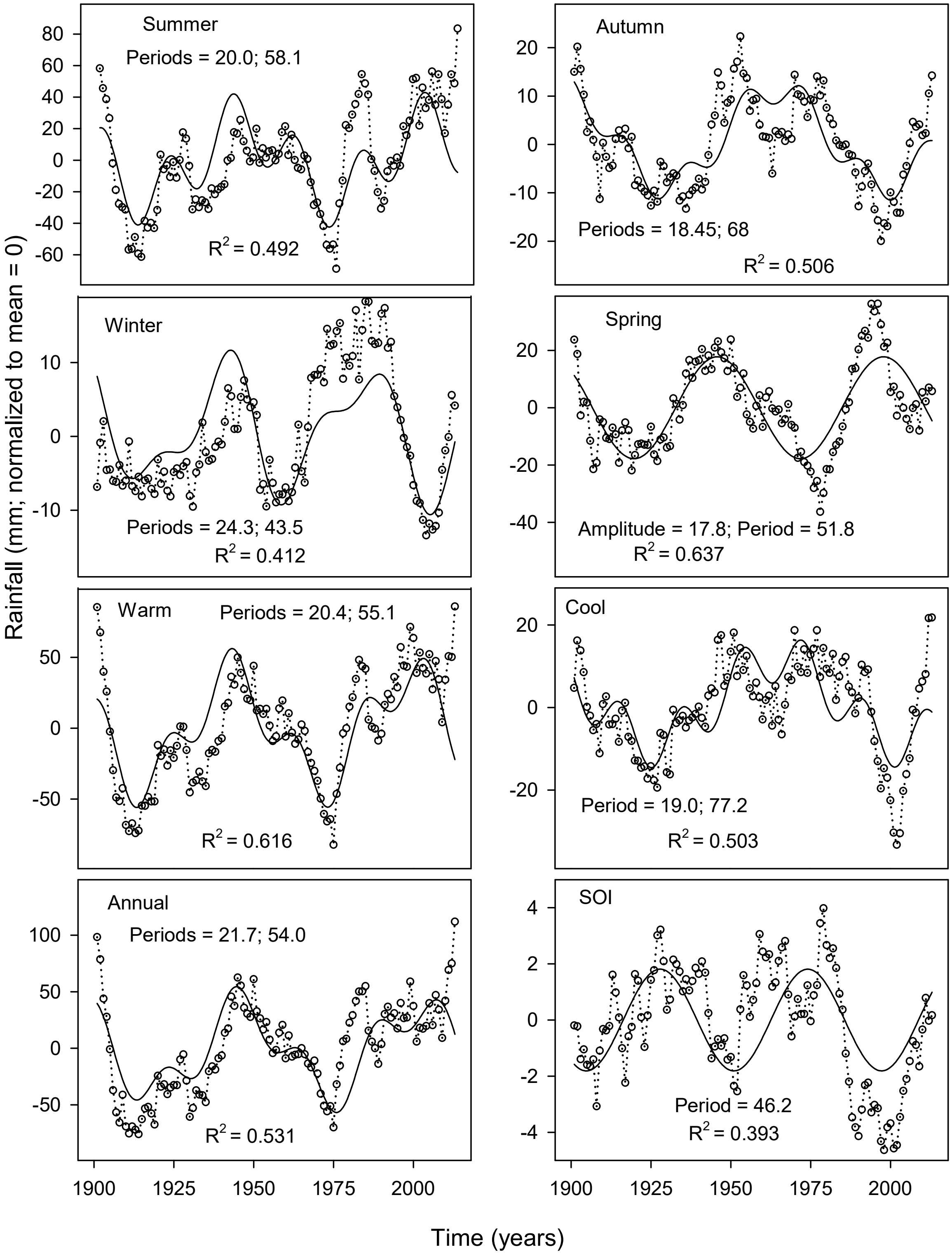


Figure 2.5. Rainfall and SOI data filtered using a 10-year simple running mean (open markers and dotted lines) fitted with single sine or double cosine wave regressions (solid lines). All regressions and all parameters' coefficients are significant (all F-values>21.7; all $p<0.0001$). Each dot represents the previous 10 years' data.

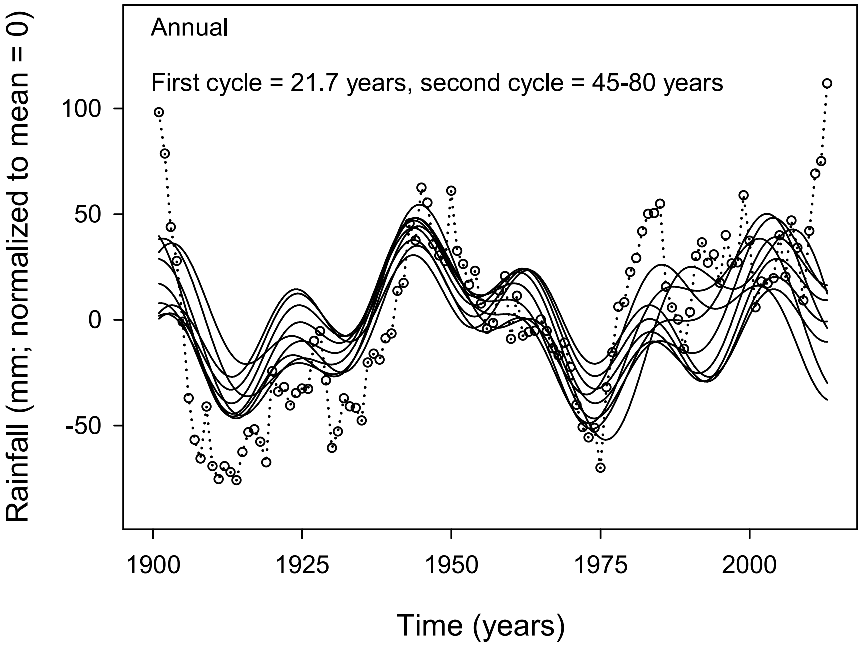


Figure 2.6. Annual rainfall data filtered using a 10-year simple running mean (open markers and dotted lines) fitted double cosine wave regressions (solid lines) with a constant short-term cycle and a long-term cycle ranging from 45–80 years. All regressions are significant (all F-values>2.6; all $p<0.02$). Each dot represents the previous 10 years' data.

2.3.3 Rainfall seasonality and concentration

Seasonality of precipitation fluctuated over time, with peak rainfall ranging from 23 December (in 1993) to 7 February (in 1973). Until 1970, peak rainfall was always during January; during the mid- to late-1970s the rainfall season shifted into February, followed by a sharp shift over during the late 1970s and 1980s to a late-December season. More recently, rains have returned to a mid-January season (Figure 2.7). The frequency of the cycle (50.6 years) is in general agreement with the long-term cycles found for rainfall amount and SOI (Figure 2.5).

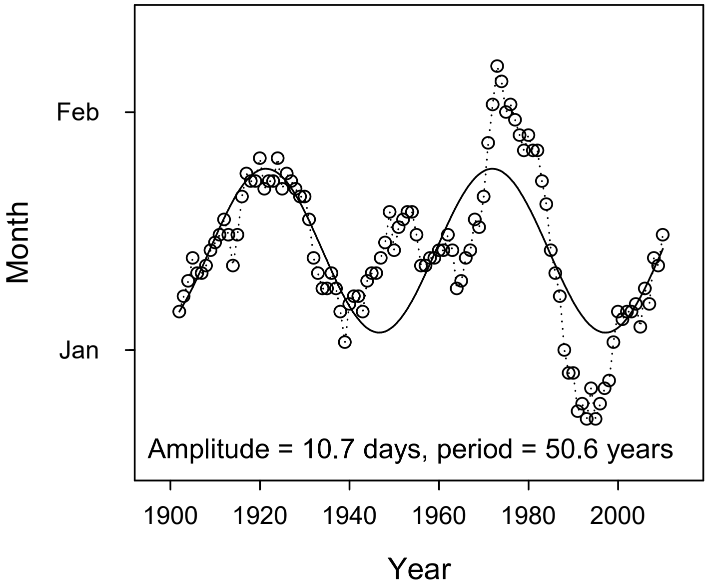


Figure 2.7. Rainfall seasonality over time. Each point reflects average values from the previous 15 years. The solid line is a sine wave regression ($F_{2,106} = 72.0, p<0.0001, R^2 = 0.576$).

Segmented regression analysis revealed two distinct trends in rainfall concentration over time (Figure 2.8). First, concentration decreased slightly over time until 1988, whereafter it increased rapidly ($F_{1,106} = 81.3$, $p<0.01$). This indicates that before 1988 rainfall became progressively but slowly more evenly spread over the year but since then it has become more concentrated. There is also evidence that there is a cycle to rainfall concentration of approximately 26 years, although this value does not match the cycles of seasonal rainfall.

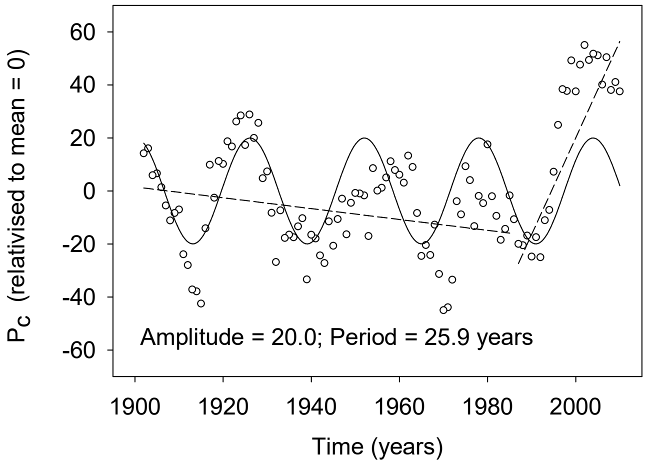


Figure 2.8. Rainfall concentration index (P_c) over time and segmented regression (dashed line). The solid line is a sine wave regression ($F_{2,106} = 29.6$, $p<0.0001$, $R^2 = 0.358$).

2.4 Conclusion

All analyses indicate that the rainfall amount, concentration, and seasonality are not random processes. The general theme that emerges is one of cyclicity, where rainfall parameters are explained as single or double cycles, often related to a period of either approximately 20 years, or in the region of 40–60 years. The only apparent shift, or directional change, appears to be rainfall concentration, which has increased significantly since 1988.

Rainfall over the past 30 years (1981–2010) was considerably higher (annual mean = 413 mm) than for the preceding 81 years (annual mean = 347 mm; 1899-1980). While this does not signal a net increase in rainfall, it has been associated with significant increases in grassiness on some long-term trials (du Toit, 2013). In contrast, regressions predict that total rainfall will decrease until about 2025 to levels similar to those experienced during the droughts of the 1910s and 1960s. This would coincide with rain falling later in the season, and possibly with increased winter rainfall. Ecologically this should induce a shift towards lower biomass production (and lower livestock carrying capacity), reduced grassiness, and increased abundance of shrubs.

The analysis of the Grootfontein rainfall data provides a detailed description of the patterns of precipitation at a site, and could act as a precedent for investigating precipitation history at other sites. Such further analyses would provide detailed and comparable descriptions of rainfall history which could then be aggregated to provide a more general understanding of rainfall at a spatial scale. The analysis also reveals that assessing possible effects of climate change on rainfall in semi-arid climates may be difficult unless (i) such effects are of significant magnitude, (ii) effects are novel (e.g. a shift to winter rainfall at Grootfontein), or (iii) significantly longer data sets are available.

CHAPTER 3 INTERACTIONS OF GRAZING AND RAINFALL ON VEGETATION AT GROOTFONTEIN IN THE EASTERN KAROO

3.1 Introduction

Rainfall and grazing are two important drivers of semi-arid rangeland composition and functioning, and considerable management and research emphasis is placed on these interacting factors to optimise livestock production (Searle *et al*. 2009). The Nama-Karoo Biome, a semi-arid grassy dwarf shrubland in the South African interior, experiences primarily summer rainfall across a gradient of mean annual precipitation (MAP) from approximately 100 to 385 mm (Mucina *et al*. 2006a). In the east and north-east of its geographic range, the biome transitions in response to increasing rainfall into semi-arid grassland. Pollen records in sedimentary rocks suggest that fluctuations in rainfall have likely determined the position of the boundary between the Nama-Karoo and Grassland Biomes over the long term (250 000 years), with grassland occurring further to the west in times of high rainfall and moving east during drier times (Scott 1989; Mucina *et al*. 2006a; Scott *et al*. 2012). An implication is that the eastern Karoo is subject to 'biome shifts', being either grassland or Nama-Karoo at any one time. Tidmarsh (1957) opined that the area had "grassveld soils … over which at present a Karoo climate prevails", presumably suggesting that the Karroid condition is not the norm. Quite what distinguishes Grassland from Karoo has not been defined, though we can infer that a key feature of the Grassland Biome is the absence (or near-absence) of Karroid dwarf shrubs (Mucina *et al*. 2006a; b; Rutherford *et al*. 2012).

The seasonal distribution of rainfall can also influence the abundance of grasses and shrubs (O'Connor and Roux, 1995). Karoo grasses have been shown to be highly responsive to summer rainfall, particularly in the eastern regions where rainfall is higher, and good summer rains can greatly increase grass growth. Increased summer rainfall increases the growth rate of existing growing plants, but may also allow dormant tillers to sprout and grass seeds in the soil seedbank to germinate (Cowling and Roux 1987). The response of Karroid shrubs to rainfall is less well understood, and while increased rainfall can promote increased shrub growth, it may also allow grasses a competitive advantage over shrubs, thereby reducing the latter's abundance (Hoffman *et al*. 1990).

Most of the Nama-Karoo is used for livestock production, primarily sheep but also goats and cattle, and to a lesser extent for conservation and game farming. The potential of the area was recognised early on (Andrew, 1889), as was the potential for livestock to cause degradation (Shaw, 1873) which in turn constrained potential animal production. In 1920, following several years of drought, a commission was established to investigate how farming practices should be changed to prevent drought losses: a central finding was that farmers were overstocked and this caused over-grazing, "*the evils of which are cumulative and apparently, not generally recognised* " (du Toit *et al.*, 1923). Research conducted subsequently has revealed that heavy stocking, or stocking continuously or repeatedly in the summer months, is particularly damaging to veld, with unpalatable and short-lived species being favoured at the expense of palatable and perennial species (both grasses and dwarf shrubs) (Dean *et al*. 1995). Whilst perennial and palatable species might not be totally extirpated from a severely grazed system (O'Connor and Roux, 1995), with species occurring as heavily grazed plants or as seeds in the seedbank, the presence of livestock prevents their growth and proliferation. This top-down control of such populations is termed the 'herbivore trap' (*sensu* Midgley and Bond 2001).

The impacts of grazing can persist after grazing has ceased. These 'legacy effects' (Cuddington, 2011) are manifest in the inability of Karoo veld to recover even over an extended period. The reason that grazing can leave such a legacy can be related to soil chemistry (Cowling 1986), surface compaction (Visser *et al*. 2004), soil seed banks (Jones and Esler, 2004), or the development of persistent stands of unpalatable shrubs (Squires and Trollope, 1979; Roux and Vorster, 1983a). In the Succulent Karoo, Seymour *et al*. (2010) found that, under conditions of 20 years' exclusion of herbivores and several years of above-average rainfall, rangeland condition improved but the degree of recovery was inversely related to historical grazing intensity; this provides an example of grazing legacy effects. However, high rainfall remains a potent determinant of rangeland condition, and grassiness in particular (Milton and Hoffman 1994; Milton *et al*. 1995; O'Connor and Roux 1995). Therefore, it is anticipated that eastern Karoo vegetation will increase in grassiness, and eventually shift from Nama-Karoo to grassland if rainy conditions persist, but that this process will take longer at sites with a history of heavy grazing. Alternatively stated, the first areas that would shift to grassland under persistent conditions of increased annual rainfall would be those with a history of lenient grazing.

Grootfontein lies in the ecotone between the Nama-Karoo and Grassland Biomes. Being in an ecotone means that small changes in rainfall may induce large changes in vegetation, to the point that an increase in rainfall might prompt a biome shift from Nama-Karoo to semi-arid grassland. Starting in the 1930s, various long-term grazing trials were established (some remain) to better understand the interactions of veld type, grazing by livestock, and rainfall on vegetation dynamics and livestock productivity. Treatments deemed to be of particular importance were season of grazing (e.g. summer *versus* winter *versus* continuous grazing), and different types of rotational grazing systems (e.g. 3-camp *versus* 6-camp), and to a lesser extent stocking rate. The Camp 6 Trials were initiated in 1934 and continue to present-day (destocked since 2010 but set to resume). The Seligman Old Block Trials were established in 1941 and terminated in 1985; all internal fences were removed and the area was stocked rotationally with cattle at a relatively low stocking rate (i.e. a comparatively benign treatment). The sites, and district in general, experienced a period of above-average rainfall (though interspersed with occasional droughts) from the mid-1970s to the mid-2010s (du Toit 2014; du Toit and O'Connor 2014). Data from identical (or nearly) treatments from these two trials afford a unique opportunity to examine vegetation changes over approximately 45 years under various livestock grazing regimes across an increasing rainfall trend.

In particular, we addressed the following hypotheses of vegetation change.

1. Degraded (severely grazed) veld will improve in condition with dwarf shrubs well represented following lenient grazing management, while veld that was leniently grazed will shift to grassland (grazing legacy effect);
2. Continued severe grazing maintains veld in its degraded condition, independent of rainfall (herbivore trap effect), while severe grazing followed by lenient grazing leads to improvement in condition;
3. Historically leniently grazed sites will incur a biome shift to grassland while historically severely grazed sites will shift to grassy shrubland (biome shift effect).

3.2 Methods

3.2.1 Study site

The study took place at the Grootfontein Agricultural Development Institute (31.4717°S, 25.0260°E) (Figure 3.1) located in the Eastern Upper Karoo (Vegetation Type: NKu4) (Mucina *et al*. 2006a). Vegetation is grassy dwarf shrubland comprising numerous growth forms, the most common perennial forms being tufted grasses, non-succulent dwarf shrubs, succulent dwarf shrubs, stoloniferous grasses, and geophytes (du Toit *et al*. 2014). Annual and biennial grasses and various ephemeral species irrupt following rains (O'Connor and Roux, 1995). Mean annual precipitation, occurring almost solely as rain, is 372 mm, approximately 60% of which falls in the summer (December – March) (du Toit and O'Connor 2014, 2016a). There is evidence of rainfall cyclicity over the past 120 years, with above-average rainfall of 426 mm per year falling from 1985-2012 (du Toit and O'Connor 2014). Growth of plants, and C_4 grasses in particular, is limited by rainfall and by the long frost season which occurs on average from mid-April to mid-October (du Toit and O'Connor 2016b). The Camp 6 and the Seligman trials are approximately 1.4 km apart, both on slightly sloping ground (between 1.5 and 2%).

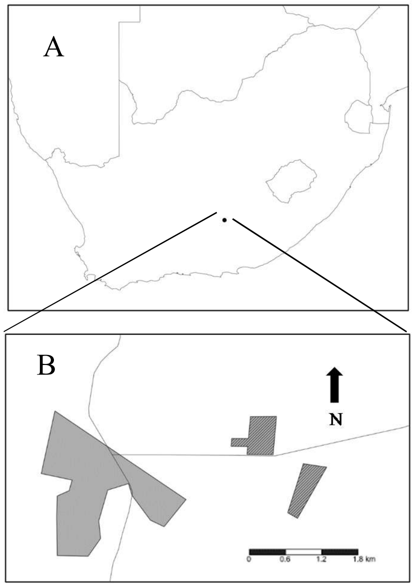


Figure 3.1. Location of Grootfontein in South Africa (A) and the locations of Middelburg (left shaded), and the Camp 6 (upper right shaded) and Seligman (lower right shaded) grazing trials (B)

3.2.2 Treatments

Treatments at Camp 6 focus mainly on season of grazing, and at Seligman mainly on types of rotational grazing systems. Several treatments are closely similar; for the purpose of this study each site has been classified as a Severe or a Lenient grazing treatment in terms of the effect that animals have on the vegetation (Donaldson, 1986; O'Connor and Roux, 1995) (Table 3.1). In addition to livestock, all sites would have been grazed lightly and occasionally by indigenous mammals.

Table 3.1. Treatments from two grazing trials at Grootfontein used to address the three hypotheses. "Recommended stocking rate" refers to long-term stocking rates, not stocking rate during the grazing period only

Grazing Trial	**Leniently grazed treatments**		**Severely grazed treatments**	
	Name	Description	Name	Description
Camp 6 (Treatments applied from 1934 to 2009)	Exclosure	Excluded from grazing by livestock since 1934 (1 replicate)	Continuous	Stocked continuously with sheep at the recommended stocking rate from 1934-2009, rested to present-day (2 replicates)
	Winter grazing	Grazed at recommended stocking rate during the winter months (April – August) from 1934-2009 (1 replicate)	Summer grazing	Grazed at recommended stocking rate during the summer months from 1934-2009 (2 replicates)
Seligman (Treatments applied from 1941 to 1985)	Exclosure	Grazing by livestock excluded from 1941-1985. Grazed at the recommended stocking rate by cattle since 1986 (1 replicate)	Continuous	Stocked continuously with sheep at the recommended stocking rate from 1941-1986. Grazed at the recommended stocking rate by cattle since 1986 (1 replicate)
	Winter grazing	Grazed at a light stocking rate during the winter months (May-September) from 1941-1985. Grazed at the recommended stocking rate by cattle since 1986 (2 replicates)	Summer grazing	Grazed at the recommended stocking rate during the summer months (November to March) from 1941-1985. Grazed at the recommended stocking rate by cattle since 1986 (2 replicates)

To address the grazing legacy hypothesis, data from Lenient and Severe treatments from 1965 and 2012 at the Seligman site were used; the herbivore trap hypothesis used data from all Severe treatments from the 1960s and 2010s (location is a confounding factor). For the biome shift hypothesis, data from all Lenient treatments and the Seligman Severe treatments from 1965 and 2012 were used.

3.2.3 Rainfall

Monthly rainfall data that span the period under observation are available for Grootfontein from a site approximately 4.5 km from the trials. Seasonal (July of year n to June of year n+1) were analysed using regression analysis to quantify long-term trends. Data for the 10-year periods prior to each set of measurements (i.e. 1966 and 2012) were compared using 2-tailed t-tests. The cumulative deviation from the mean was calculated to identify general trends in rainfall.

3.2.4 Vegetation data and analysis

Plots were sampled sporadically during the 1940s-1960s in winter using the wheel-point method of Tidmarsh and Havenga (1955), and again using the same equipment in 2011 (Camp 6) and 2012 (Seligman). Between 500 and 3000 points were collected per plot, depending on plot size. The response variable was basal cover, expressed as a percentage, where the plant species was recorded if the metal pin encountered the base of a plant. This excludes canopy encounters and nearest plants. Owing to the higher relative basal cover of grasses than shrubs, the method is known to overestimate grass abundance and underestimate shrub abundance (Stuart-Hill and Hobson, 1991). Data from 1965 and 2012 (Seligman) and 1966 and 2011 (Camp 6) were used.

Compositional data of perennial species were analysed using non-metric multidimensional scaling (NMS), using the Bray-Curtis distance coefficient, an ordination technique that allows all variation within the data to be accommodated within a set number of axes. We selected two axes in order to identify, firstly, any major shifts predicted within our hypotheses, and, secondly, to understand variation in composition external to these main trends (Holland, 2008; Wildi, 2013). Non-metric multidimensional scaling is useful when analysing ecological data where assumptions about its nature (e.g. linearity) cannot be made. The significance of the stress value was evaluated following the method of Sturrock and Rocha (2000). An ordination-based approach was used owing to limited replication and because location was sometimes a confounding factor.

3.2.5 Growth forms, species and classes

All species were described in terms of growth form, and changes over time of the most dominant growth forms were calculated. Constituent species of each dominant growth form, along with several abundance parameters, were calculated.

Vegetation along a gradient of degraded Karoo to grassland was classified into one of four classes based on the proportion of grass to shrubs and the basal cover of either grass or shrubs. In the absence of an existing classification system we devised one based on several assumptions using existing research findings as a guide.

1. **Degraded Nama-Karoo** has a very high proportion of dwarf shrubs, and a very low cover of perennial grass (proportion of perennial grass <10%, basal cover of grass < 0.5%) (Milton and Hoffman, 1994);
2. **Grassland** has a very high proportion of perennial grass (>90%), and an (near) absence of dwarf shrubs (basal cover < 0.5%) (Mucina *et al*. 2006a);
3. **Grassy Karoo** resembles Grassland by having a very high proportion of perennial grass (> 90%), but also contains a notable cover of shrubs (basal cover ≥0.5%)
4. **Normal Nama-Karoo** is a default for all other combinations (proportion of perennial grass 90%≥x≥10%, basal cover of shrubs ≥0.5%).

Cut-off values were arbitrary but designed to minimise the chance of 1) falsely classifying Normal Nama-Karoo as Degraded Nama-Karoo, 2) falsely classifying Normal Nama-Karoo as Grassy Karoo or Grassland, and 3) falsely classifying Grassy Karoo as Grassland.

3.3 Results

3.3.1 Rainfall

Seasonal rainfall (July of year n to June of year n+1) showed an overall linear increase of 12.9 mm per decade from approximately when the trials were initiated in 1934 to 2012 ($F_{1,77}$=4.64, P=0.034), with rainfall over the ten years prior to the first measurements (1957-1966) significantly lower (average = 350 mm) than those prior to the second measurements (2003-2012; average = 491 mm; t_{18}=3.11, P<0.01)) (Figure 3.2A). Furthermore, from the mid-1940s until the early 1970s there had been a relatively fast decline in rainfall (accrued deficit of 1350 mm over 37 years), after which rainfall increased slowly until 2005 (accrued surplus of 300 mm over 34 years) and then rapidly thereafter (accrued surplus of 1050 mm over 6 years) (Figure 3.2B). The main turning point occurred in the mid-1970s, when rainfall averaged 527 mm from 1973-1976, whereas during the previous ten years the average had been 290 mm.

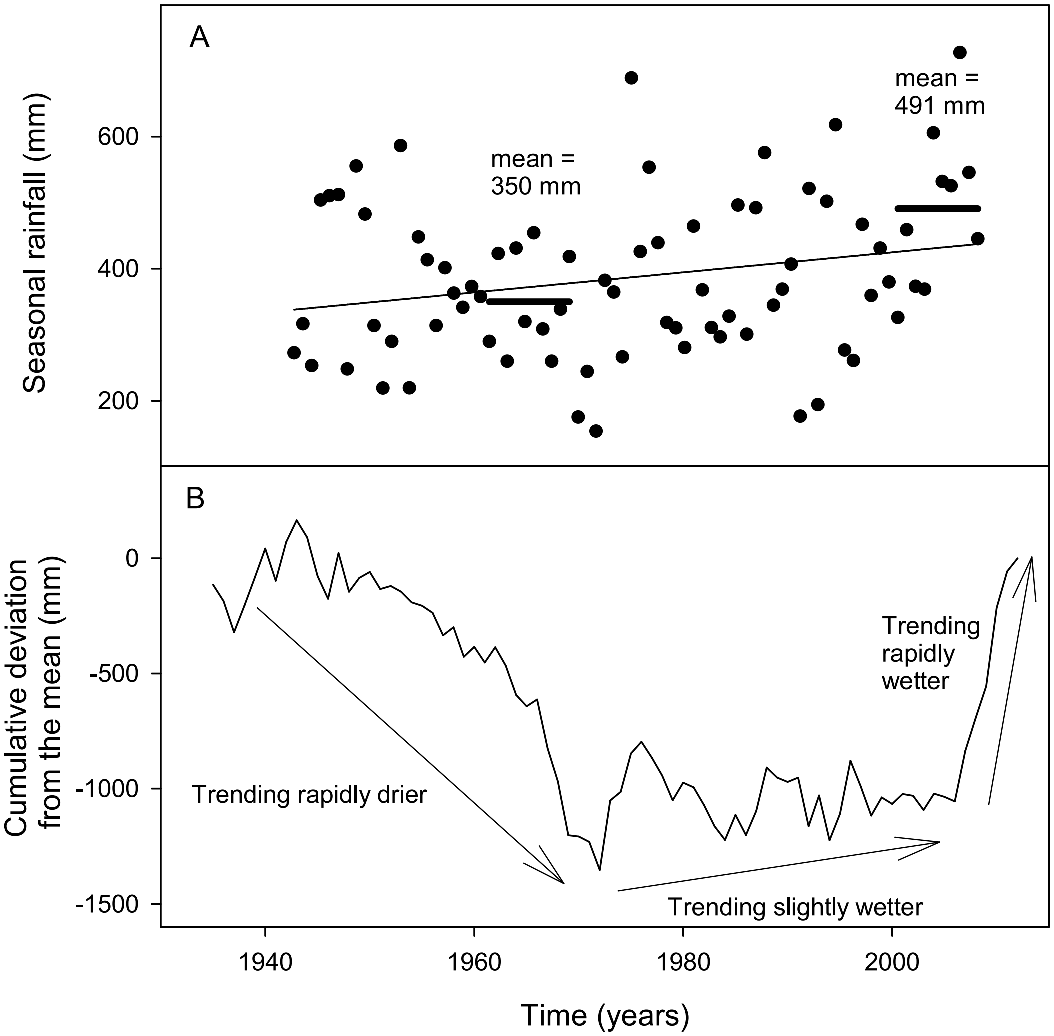


Figure 3.2. A: Seasonal rainfall from 1935-2012 at Grootfontein with linear regression fitted (thin solid line; y = 1.29x -2158). Average seasonal rainfall for the ten years before the early surveys (1957-1966) and late surveys (2003-2012) are shown (thick solid horizontal lines); B: Cumulative deviation from the mean seasonal rainfall at Grootfontein, highlighting general trends in rainfall.

3.3.2 Growth forms and species

The most dominant growth forms, comprising 73% of all species (54 of 74) and 96.1% of all plants, were perennial dwarf shrubs (30 species), annual or perennial grasses (i.e. grasses that can be either annual or perennial) *sensu* Germishuizen and Meyer (2003) (2 species), perennial grasses with a high grazing value (hereafter 'palatable') (10 species), perennial grasses with a low grazing value (hereafter 'unpalatable') *sensu* Botha *et al*. (2001) (9 species), and perennial shrubs (1 species) (Table 3.2). Other growth forms included annual herbaceous cyperoids (1 species), annual dwarf shrubs (1 species), perennial parasitic dwarf shrubs (1 species), perennial succulent dwarf shrubs (3 species), annual grasses (3 species), perennial herbaceous geophytes (1 species), herbaceous annuals (2 species), herbaceous biennials (1 species), herbaceous perennials (5 species), perennial succulents (1 species), and 1 species identified only to genus level that could not be placed in any of the previous groups.

Overall basal cover increased approximately three-fold from 5.0 to 16.5% between the 1960s and 2010s. Patterns of change of the abundance of growth forms from the 1960s to the 2010s were generally similar across Severe and Lenient sites (Figure 3.3). Woody perennials (shrubs and dwarf shrubs) decreased to approximately 30% of their original abundance. Many of the most abundant shrubs in the 1960s, including the highly unpalatable *Chrysocoma ciliata* and the moderately-palatable *Eriocephalus* species and *Pentzia incana*, were not encountered in the 2010s. All grass growth forms increased considerably. Annual/perennial grasses (comprising mostly *Aristida congesta*) increased approximately twelve-fold, unpalatable grasses four-fold (mainly *Eragrostis lehmanniana* and *Aristida diffusa*), and palatable grasses nearly sixty-fold. The large, productive and highly palatable species *Heteropogon contortus* and *Sporobolus fimbriatus* showed wide-spread colonisation, being encountered in only one paddock in the 1960s and nearly all the paddocks in the 2010s. *Themeda triandra*, a species that occurs less often than expected in the Karoo owing possibly to historical overgrazing and subsequent low dispersal (Smith and Yeaton 2005), colonised in large near-monospecific patches, attaining a high basal cover of nearly 12% in one paddock.

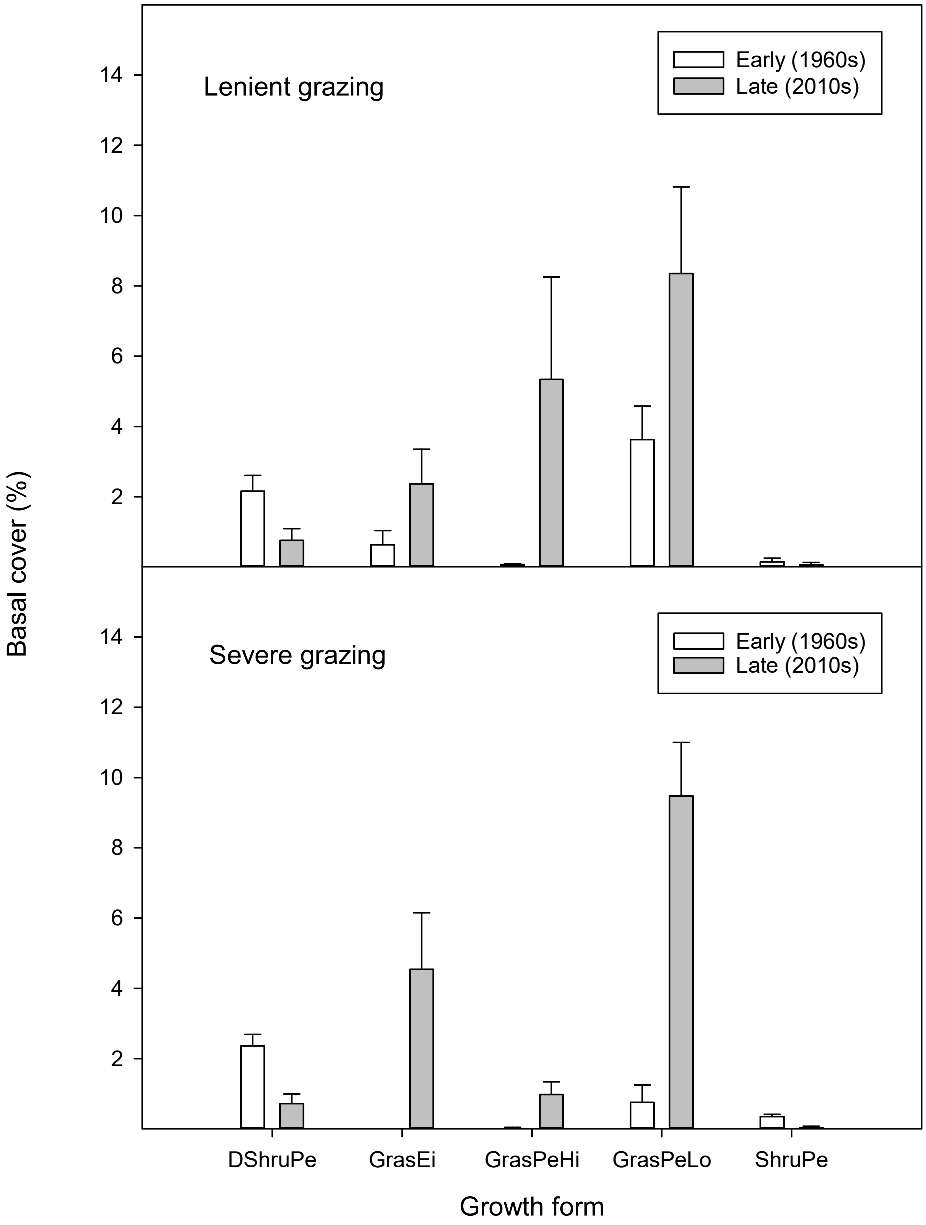


Figure 3.3. Mean basal cover of the five dominant growth forms on Lenient and Severe treatments in the 1960s (open) and 2010s (shaded) at Grootfontein. DShruPe = perennial dwarf shrubs, GrasEi = annual/perennial grasses, GrasPeHi = palatable perennial grasses, GrasPeLo = unpalatable perennial grasses, ShruPe = perennial shrubs. Bars show 1 standard error.

Table 3.2. Values of various parameters of all species in the five most common growth forms at Grootfontein. Species referred to in the text are shaded in grey

Species	GIV[1]	NumE[2]	NumL[3]	AvgE[4]	AvgL[5]	MaxE[6]	MaxL[7]
Perennial Dwarf Shrubs							
Amphiglossa triflora	0	3	2	0.04	0.01	0.2	0.1
Aptosimum elongatum	0	0	1	0	0	0	0.03
Blepharis mitrata	1	2	2	0.01	0.01	0.1	0.1
Chrysocoma ciliata	1.5	8	0	0.58	0	2.85	0
Eriocephalus ericoides	5	8	0	0.36	0	2	0
Eriocephalus spinescens	4.5	6	0	0.08	0	0.3	0
Felicia fascicularis	6.2	0	1	0	0.02	0	0.2
Felicia filifolia	5.9	0	4	0	0.11	0	0.5
Felicia muricata	6.5	6	2	0.18	0.18	1.4	1.7
Galenia procumbens	4.3	1	0	0	0	0.05	0
Helichrysum dregeanum	6.3	1	1	0.01	0.04	0.1	0.4
Helichrysum lucilioides	5.2	1	2	0.01	0.05	0.1	0.45
Helichrysum rutilans	3.3	0	1	0	0	0	0.05
Helichrysum zeyheri	4.1	0	4	0	0.03	0	0.1
Hermannia pulchella	2.7	0	1	0	0.01	0	0.1
Melolobium microphyllum	4.3	0	1	0	0.01	0	0.1
Nenax microphylla	4.3	1	2	0.01	0.01	0.1	0.1
Osteospermum leptolobum	4.6	0	1	0	0.03	0	0.3
Pentzia globosa	4.8	1	1	0.02	0	0.2	0.05
Pentzia incana	5.7	7	0	0.7	0	2.2	0
Phymaspermum parvifolium	6.2	4	2	0.07	0.02	0.47	0.2
Pteronia glauca	3.2	3	0	0.03	0	0.2	0
Pteronia glomerata	3.9	1	0	0.02	0	0.2	0

Species	GIV[1]	NumE[2]	NumL[3]	AvgE[4]	AvgL[5]	MaxE[6]	MaxL[7]
Pteronia sordida	4.5	5	0	0.04	0	0.2	0
Rosenia humilis	3.5	5	4	0.04	0.03	0.2	0.1
Salsola calluna	7.2	1	0	0.05	0	0.6	0
Selago saxatilis	2	2	5	0.02	0.07	0.1	0.6
Solanum tomentosum	0	0	1	0	0.07	0	0.8
Stachys aurea	1.4	2	4	0.01	0.02	0.05	0.07
Wahlenbergia tenella	3	0	1	0	0	0	0.05
Annual/perennial grasses							
Aristida congesta	1.3	4	11	0.29	3.54	2.2	10.7
Enneapogon desvauxii	1	0	1	0	0.01	0	0.1
Perennial palatable grasses							
Cymbopogon pospischilii	7.6	0	1	0	0.01	0	0.1
Digitaria eriantha	8.9	0	3	0	0.37	0	2.07
Eragrostis conferta	6.9	0	2	0	0.05	0	0.4
Eragrostis curvula	6.7	1	4	0.01	0.05	0.07	0.3
Fingerhuthia africana	6.6	1	3	0.01	0.31	0.1	1.8
Heteropogon contortus	7.2	1	8	0.01	0.47	0.1	2.7
Hyparrhenia hirta	6.3	0	1	0	0	0	0.05
Sporobolus fimbriatus	9.5	1	7	0.01	0.13	0.1	0.5
Stipagrostis obtusa	6.6	1	0	0.01	0	0.1	0
Themeda triandra	9.3	0	2	0	1.09	0	11.7
Perennial unpalatable grasses							
Aristida diffusa	5.1	3	10	0.17	2.64	0.95	8.55
Cynodon incompletus	4.1	0	3	0	0.11	0	0.6
Enneapogon scoparius	4.4	3	7	0.06	1.21	0.45	6.65

Species	GIV[1]	NumE[2]	NumL[3]	AvgE[4]	AvgL[5]	MaxE[6]	MaxL[7]
Eragrostis bergiana	2.8	3	0	0.05	0	0.3	0
Eragrostis bicolor	6	1	0	0.01	0	0.13	0
Eragrostis lehmanniana	5.4	7	11	0.75	4	4.05	12.67
Eragrostis obtusa	4	2	4	0.03	0.07	0.2	0.3
Oropetium capense	1.3	1	4	0.01	0.12	0.1	0.7
Tragus koelerioides	2.2	9	9	0.98	0.81	2.8	3.4
Perennial shrubs							
Lycium spp	1.6	7	2	0.19	0.04	0.55	0.2

[1] GIV = Grazing Index Value following Botha *et al*. (2001)

[2] NumE = Number of paddocks where the species was encountered – Early (1960s)

[3] NumL = Number of paddocks where the species was encountered – Late (2010s)

[4] AvgE = Average basal cover (5) across all 11 paddocks – Early (1960s)

[5] AvgL = Average basal cover (5) across all 11 paddocks – Late (2010s)

[6] MaxE = Maximum basal cover in one paddock – Early (1960s)

[7] MaxL = Maximum basal cover in one paddock – Late (2010s)

3.3.3 Grazing legacy effect

In 1965, there were clear differences between the compositions of the Severe (all Degraded) and the Lenient sites (all Normal) (Figure 3.4), reflecting the treatments that were applied at the time. In the Severe sites, the most common species were the highly unpalatable shrub *Chrysocoma ciliata*, the grazing-tolerant *Pentzia incana*, and the short, creeping grass *Tragus koelerioides*, while the Lenient sites were dominated by *Eragrostis lehmanniana*, *Tragus koelerioides*, and *Pentzia incana*. By 2012, there had been a major compositional shift. Severe sites had changed to being Normal, Grassy or Grassland, and Lenient sites to Normal, Grassy or Grassland. The three most common species in 2012, for both Severe and Lenient sites, were *Eragrostis lehmanniana*, *Aristida diffusa* (a large, tufted, unpalatable grass), and *Tragus koelerioides*. Species composition in the Lenient sites had a higher variability than those at the Severe sites. At all the Severe sites in 2012, the most common species was *Aristida diffusa*;

this was never the case at the Lenient sites. Thus, the grazing legacy effect is evident in that historically severely grazed sites are more similar to each other than leniently grazed sites, and are dominated by *Aristida diffusa*.

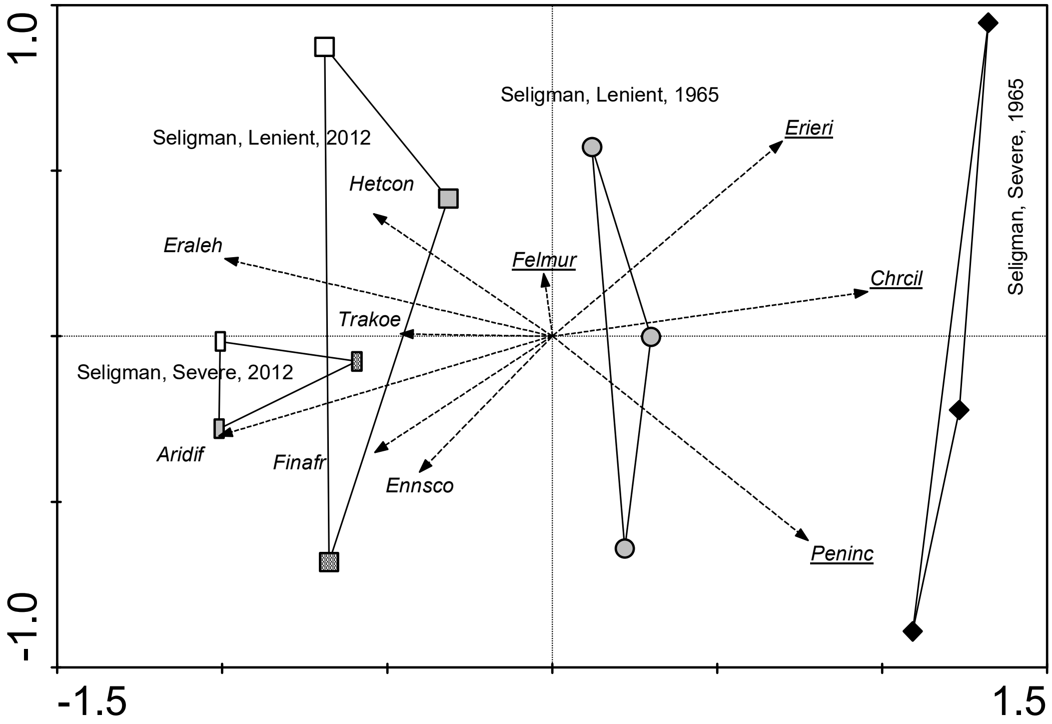


Figure 3.4. Non-metric multidimensional scaling of Bray-Curtis distances among sites grazed severely (diamonds) or leniently (circles) in 1965, and those same sites in 2012 (rectangles and squares, respectively) following lenient grazing since 1985. Colours of markers represent Degraded (black), Normal (grey), Grassy (hashed) and Grassland (white) vegetation types. Species, overlaid as supplementary variables, are grasses (not underlined) or dwarf shrubs (underlined). (Erieri = *Eriocephalus ericoides*, Chrcil = *Chrysocoma ciliata*, Peninc = *Pentzia incana*, Ennsco = *Enneapogon scoparius*, Finafr = *Fingerhuthia africana*, Aridif = *Aristida diffusa*, Trakoe = *Tragus koelerioides*, Eraleh = *Eragrostis lehmanniana*, Hetcon = *Heteropogon contortus*, Felmur = *Felicia muricata*.) Stress = 0.113, $P < 0.01$.

3.3.4 Herbivore trap effect

In the 1960s the Severe Seligman sites were all Degraded, and the Severe Camp 6 sites were Degraded (1) or Normal (2). By the 2010s all sites had undergone a major shift in composition (Figure 3.5), with Seligman sites becoming Normal, Grassy, or Grassland, and Camp 6 sites becoming Grassy (2) or Grassland (1). In the 1960s the most common species were

Chrysocoma ciliata, *Pentzia incana*, and *Tragus koelerioides*, and by the 2010s the three most dominant species were *Eragrostis lehmanniana*, *Aristida diffusa*, and *Tragus koelerioides*. Differences between the Camp 6 and Seligman sites in the 2010s were slight, indicating that there was a shift to increased grassiness that was largely independent of grazing pressure.

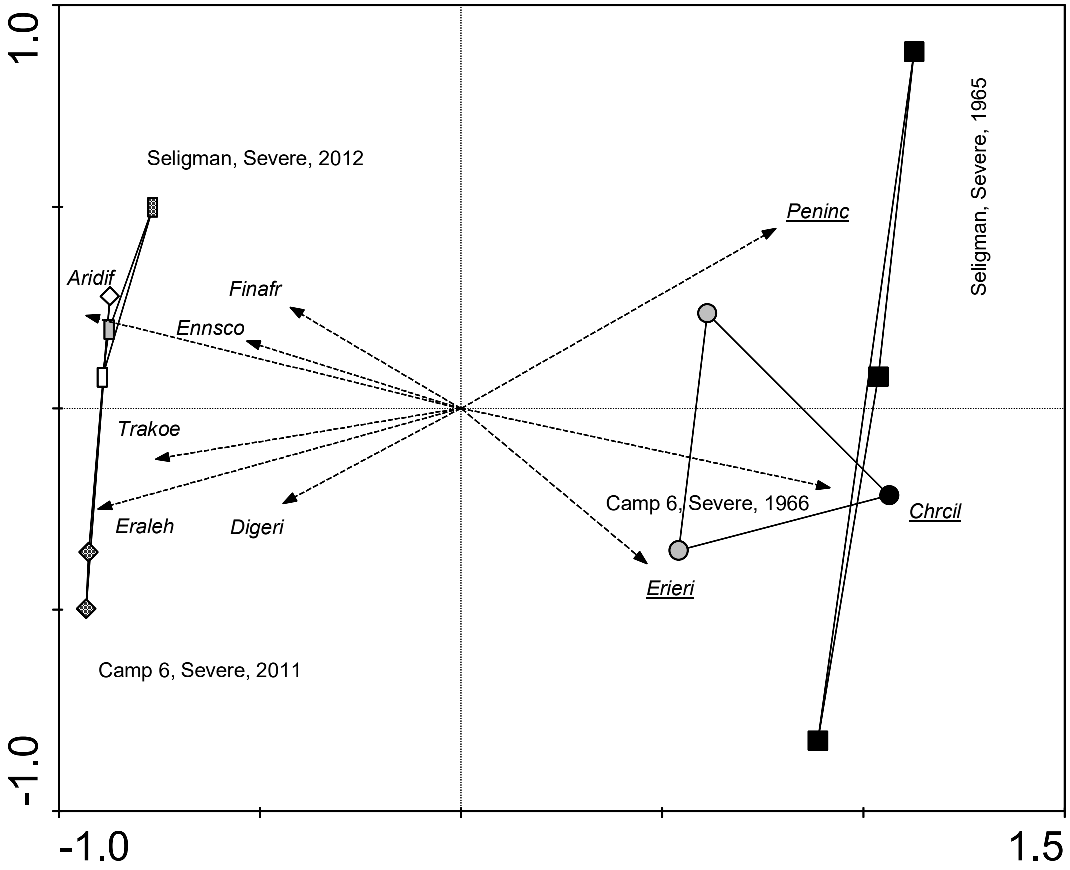


Figure 3.5. Non-metric multidimensional scaling of Bray-Curtis distances among sites at Seligman severely grazed in 1965 (squares) and following lenient grazing since 1985 (rectangles), and Camp 6 severely grazed sites in 1966 (circles) and in 2011 (diamonds). Colours of markers represent Degraded (black), Normal (grey), Grassy (hashed) and Grassland (white) vegetation types. The most abundant species, overlaid as supplementary variables, are grasses (not underlined) or dwarf shrubs (underlined). (Aridif = *Aristida diffusa*, Chrcil = *Chrysocoma ciliata*, Digeri = *Digitaria eriantha*, Ennsco = *Enneapogon scoparius*, Eraleh = *Eragrostis lehmanniana*, Erieri = *Eriocephalus ericoides*, Finafr = *Fingerhuthia africana*, Peninc = *Pentzia incana*, Trakoe = *Tragus koelerioides.*) Stress = 0.053, P < 0.01.

3.3.5 Biome shift effect

In the 1960s, Lenient sites were Normal (4) or Grassy (1), and in the 2010s were Normal (1), Grassy (2) or Grassland (2), while Severe sites in 1965 were Degraded (3) and in 2012 were Normal (1), Grassy (1) or Grassland (1) (Figure 3.6). Therefore, the biome shift effect is supported inasmuch as there have been cases of the formation of grassland, but this did not always happen, and there appeared to be no modifying influence of historical heavy grazing. Dominant species in the Lenient sites in the 1960s were *Eragrostis lehmanniana*, *Tragus koelerioides*, and *Pentzia incana*, and in the 2010s were *Eragrostis lehmanniana*, *Themeda triandra* and *Enneapogon scoparius* (medium-sized tufted grass).

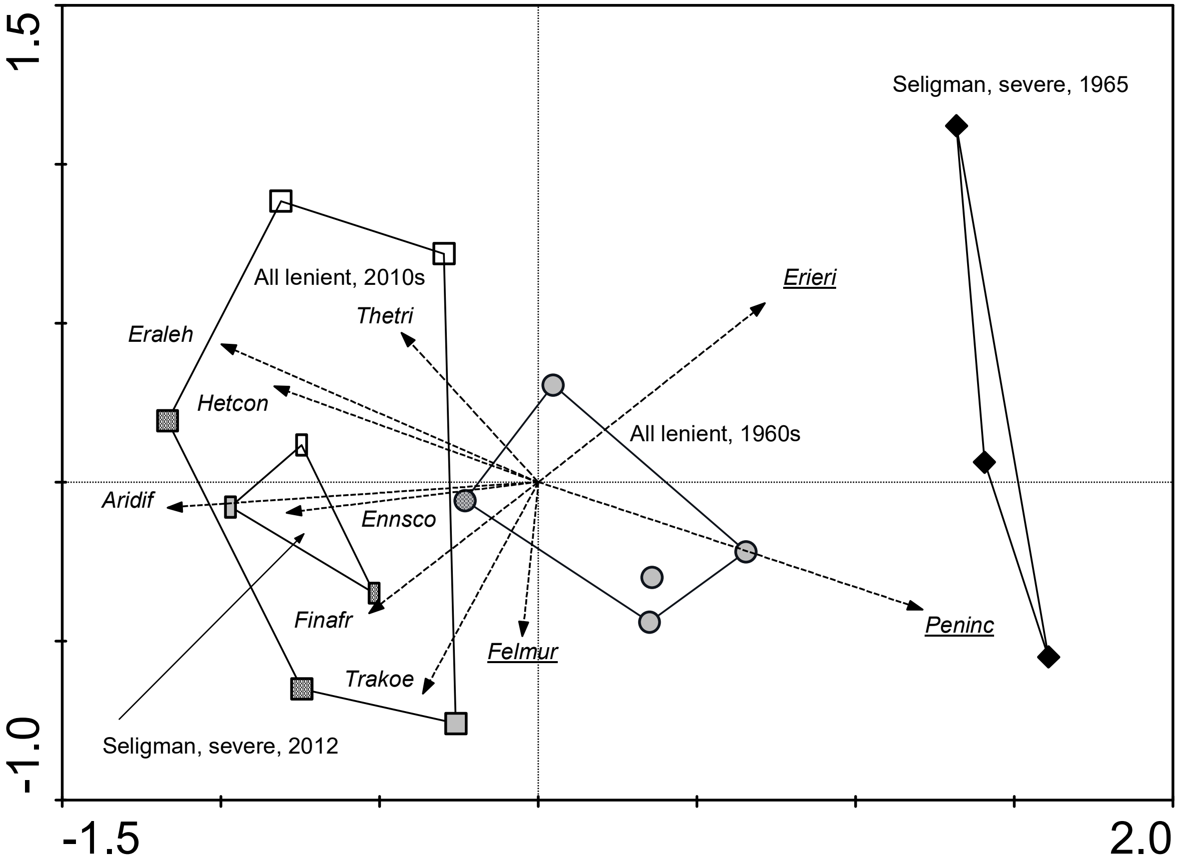


Figure 3.6 Non-metric multidimensional scaling of Bray-Curtis distances among Seligman Severe sites in 1965 (diamonds) and 2012 (rectangles) and all Lenient sites in 1960s (circles) and 2010s (squares). Colours of markers represent Degraded (black), Normal (grey), Grassy (hashed) and Grassland (white) vegetation types. The most abundant species, overlaid as supplementary variables, are grasses (not underlined) or dwarf shrubs (underlined). (Aridif = *Aristida diffusa*, Ennsco = *Enneapogon scoparius*, Eraleh = *Eragrostis lehmanniana*, Erieri = *Eriocephalus ericoides*, Felmur = *Felicia muricata*, Finafr = *Fingerhuthia africana*, Hetcon = *Heteropogon contortus*, Peninc = *Pentzia incana*, Thetri = *Themeda triandra,* Trakoe = *Tragus koelerioides*). Stress = 0.015, P < 0.01.

3.4 Discussion

Rainfall results clearly demonstrate an increasing rainfall trend from the early to the late surveys. This trend was not gradual, but rather was initiated abruptly in 1973 and accelerated in 2007. Grass abundance is limited by rainfall in the Karoo, so if the upper limit of rainfall in the typical dwarf shrub dominated Nama Karoo is about 385 mm (Mucina *et al*. 2006a), then these data would imply recent conditions would have been suitable for a significant increase in grassiness, or even a biome-shift to some form of semi-arid grassland. Additionally, rainfall generally peaked earlier in the season (i.e. midsummer) after 1985 (du Toit and O'Connor 2014, 2016a), and this would benefit perennial C_4 grasses.

The nett changes in abundance of growth forms over time were the collapse of dwarf shrubs, and the extensive colonisation by grasses. Total cover also increased considerably, which suggests that increased rainfall allowed grasses to colonise a hitherto inhospitable environment, and out-compete shrubs in the process. Elsewhere, studies have found that grasses can out-compete dwarf shrubs (Hoffman *et al.* 1990), while dwarf shrubs might not out-compete grasses and may in fact facilitate their growth (Smith 2000). Interestingly, in the 2010s the abundance of the 'pioneer' species *Aristida congesta* was very high, suggesting that there were spaces or gaps that could still be colonised by fast-growing species: perennial grasses had not saturated the environment. This is important agriculturally because *A. congesta* seeds damage wool, and it has been proposed that judicious veld management and a shift to perennial species may reduce the prevalence of this plant (Bedford and Roberts, 1975).

There was evidence in support of the grazing legacy effect at Seligman despite the increase in grassiness and collapse of dwarf shrub populations across all sites. Historically leniently-grazed sites differed compositionally much more than historically severely-grazed sites, perhaps indicating responsiveness to environmental factors such as soil type and depth. In contrast, the Severe sites showed little between-site variation, and were all dominated by *Aristida diffusa*. Thus, despite rainfall being a potent driver of vegetation composition, grazing legacy effects were evident in the composition of the new growth form (grasses) that this increased rainfall had allowed.

There was very limited evidence for the herbivore trap effect, despite some differences in composition between sites that were confounded by location. For all severely-grazed sites, there was a drastic shift in composition from Degraded or Normal dwarf shrubland to grass-dominated communities of a more uniform composition, independent of whether grazing was present or not. This points to rainfall being a powerful driver of vegetation change, dwarfing the effects of even severe grazing.

The hypothesis that leniently-grazed sites will shift to grassland was partially supported because two of the Lenient sites became grassland. Contradictory to expectation, however, was that one of the three Severe sites also shifted to grassland, suggesting that transition to grassland may be independent of initial composition and that degraded or heavily-grazed veld is as likely to become grassland as is leniently-grazed veld. An interpretation for this would be that degraded veld has a low cover, and hence more gaps available for colonisation of new grasses. Furthermore, in degraded veld there would be less competition from grasses owing to their lower abundance. Milton and Hoffman (1994) predicted that intense disturbance (e.g. drought, severe trampling) may allow extensive germination and recruitment of seedlings in the resulting competition-free environment. Therefore, Karroid vegetation in the eastern Nama-Karoo can shift to grassland, but may be prevented from doing so by other factors (we surmise that edaphic conditions may be important).

From an agricultural point of view, the transition across most sites to becoming grass-dominated can be viewed as an 'improvement' owing to the increase of palatable species, and hence forage availability to livestock. The story may be different when interpreted within the ecological principles of resistance (ability to remain unchanged) and resilience (ability to return to 'original' state). Concomitant with the increase in grassiness was a substantial decline in the populations of dwarf shrub species, suggesting low ecological resistance under good growth conditions (i.e. high rainfall). Should high summer rainfall conditions persist, as has been suggested (Engelbrecht *et al*. 2009), then a grassy eastern Karoo may become the norm. If, however, rainfall declines or the area experiences a prolonged drought, then it would be anticipated that grasses would die out, leaving behind a sparse dwarf shrubland. If so, and assuming recolonization by shrubs is not swift, this vegetation type would show weak resilience in the face of high rainfall despite its high resilience to heavy grazing and drought (Roux and Theron, 1987).

Under conditions of 'normal' rainfall variation, eastern Karoo vegetation is influenced strongly by herbivory (Roux and Theron, 1987; O'Connor and Roux, 1995). Our results here show that as rainfall increased, the effect of livestock became much reduced in terms of the composition of major growth forms and most dominant species. This suggests a shift from top-down (composition is driven by herbivory) to bottom-up (composition is driven by plant resource availability) control (Hunter and Price, 1992).

3.5 Summary and conclusion

Increased rainfall over the past several decades have induced a major increase in grassiness at the expense of dwarf shrubs at Grootfontein in the eastern Karoo across a range of leniently-and severely-grazed sites. Short-lived, unpalatable perennial and especially palatable perennial grasses have all abundantly increased. High rainfall had such a strong effect on species composition that the legacy of severe grazing was evident only in the composition of the grasses that had become dominant, not in the degree to which grasses colonised. Similarly, severe grazing was not sufficient to cause a herbivore trap that would prevent grasses becoming dominant and shrub populations collapsing. Results suggest a shift from top-down control by herbivores to bottom-up control by a directional change in rainfall. All degraded veld (induced through severe grazing) has increased in grassiness and none remains, and there are several cases of a biome shift from Nama-Karoo to Grassland (Table 3.3). The collapse of shrub populations points to a low ecological resistance to high rainfall conditions, despite being resilient in the face of grazing. Future prolonged droughts or even a return to historical rainfall regimes could result in the death of perennial grasses, leaving behind sparse shrublands.

Table 3.3. Summary of expectations and actual responses of vegetation types at Grootfontein

Hypothesis	Treatment	Expected response		Actual response	
		1960s	2010s	1960s	2010s
Grazing legacy	Leniently grazed (Seligman)	🟦	⬠	🟦	🟦 ▨ ⬠
	Severely grazed then leniently grazed (Seligman)	⬟	🟦	⬟	🟦 ▨ ⬠
Herbivore trap	Severely grazed (Camp 6)	⬟	⬟	⬟ 🟦	▨ ⬠
	Severely grazed then leniently grazed (Seligman)	⬟	🟦	⬟	🟦 ▨ ⬠
Biome shift	Severely grazed then leniently grazed (Seligman)	⬟	▨	⬟	🟦 ▨ ⬠
	Leniently grazed (Camp 6 and Seligman)	🟦	⬠	🟦 ▨	🟦 ▨ ⬠

⬟ Degraded Karoo 🟦 Normal Karoo ▨ Grassy Karoo ⬠ Grassland

CHAPTER 4 INFLUENCE OF SEASON OF GRAZING AND RAINFALL OVER TIME ON VEGETATION IN THE EASTERN KAROO, SOUTH AFRICA

4.1 Introduction

The Nama-Karoo is an inland biome in the central and western interior that covers 20.4% of South Africa and extends into south-western Namibia. Its vegetation is characterised by numerous species of the dwarf-shrub growth form within a matrix of predominantly C_4 grasses (annual and perennial), occasional shrubs and trees, geophytes, and annual herbs (Mucina, Rutherford, *et al.*, 2006). There is a general increase in grassiness from west to east, related to a gradient of increasing mean annual rainfall (Hoffman, 1989), until the biome transitions into grassland at its eastern boundary. At a site, grass cover increases with increasing rainfall (du Toit *et al.*, 2018), while shrubs are less responsive (Hoffman *et al.*, 1990). Rain falls mainly in the hot summer, with a smaller amount falling in the cool, frost-prone winter (du Toit and O'Connor, 2014, 2016b). Temperature and rainfall interact with plant growth forms, with C_4 grasses growing predominantly in the summer (notably November and December), and C_3 shrubs growing more slowly but throughout the year (predominantly during March – May and August - September) and being able to grow during the cooler half of the year when frost is common, if rain has fallen (Roux, 1963, 1966). As life forms, grasses and dwarf shrubs may compete with each other (Hoffman *et al.*, 1990). Under conditions of high rainfall, grasses may out-compete shrubs (du Toit *et al.*, 2018), while under conditions of low rainfall the cover of grasses and of dwarf shrubs appear unrelated (O'Connor and Roux, 1995). Droughts are a feature of the Karoo and severe droughts have occurred with an approximately 20-year frequency at Grootfontein over the past century (du Toit, 2017). Mortality of grasses can be high during a drought and, although dwarf shrubs are more drought-resistant, they too may be extirpated should dry conditions persist for long enough (Roux, 1965a). Records of shrub mortality as a consequence of drought are rare. One example is the mortality of the unpalatable *Chrysocoma ciliata*, although its post-drought recovery (through germination) was swift (Roux, 1965a). Wide-scale collapses in populations of *Pentzia incana* have been reported, and while soil/plant water relations were thought to have contributed to their demise, it was not during a drought per se (Roux, 1967a).

Historically, grazing pressure on plants in the Nama-Karoo was usually low, determined in part by the limited distribution of surface water available for animals (Milton, 1993; Archer, 2000).

Occasional high stocking densities of animal were achieved when huge herds of springbok trekked through the region (Roche, 2004). In the 1800s, livestock at much higher stocking rates were introduced, and numbers further increased with the advent of windmills and fencing which had become common-place by 1880 (Archer, 2000). Shaw (1873) indicates these high animal numbers had a pronounced detrimental effect on the vegetation of the Karoo. Sheep numbers in South Africa had reached approximately 5 million by the mid-1800s, doubling by 1900, and increasing to approximately 45 million by the 1930s (van den Berg *et al.*, 2019). While these numbers indicate the national flock, not the Karoo *per se*, they reflect the general patterns of increase of sheep in the Karoo. Following the droughts of the 1900-1915 period when average annual rainfall was 288 mm, well below the long-term average of 373 mm (du Toit and O'Connor, 2014), a commission of enquiry provided recommendations on controlling, *inter alia*, animal grazing patterns: "*This* [control of intensive grazing] *he* [the farmer] *can do if his farm is divided into paddocks, for such a sub-division permits of the best possible distribution of the stock over the farm, and allows of absolute rest for paddocks which require it. … Complete grazing control is the first essential of a system of stock farming that has for its purpose prevention of deterioration of the vegetal covering*" (du Toit *et al.*, 1923). These recommendations led to the establishment of the "Camp 6" grazing trials at the Grootfontein College of Agriculture near Middelburg in the eastern Karoo, which in turn spawned further trials including the "Seligman Old Block" grazing trials nearby (Tidmarsh, 1951). Results from these grazing trials led to the development of equilibrium-based models of vegetation response to grazing and rainfall (Vorster and Roux, 1983; Moll and Gubb, 1989), which in turn informed governmental policy and provided guidance to farmers on how best to manage veld.

A key finding was that repeatedly grazing in the same season can strongly influence vegetation composition. Gill (1939) reports that after five years of repeated summer grazing at Camp 6 (mid-December to mid-April each year), perennial grasses had largely been extirpated, palatable shrubs were heavily grazed, and large bare patches had formed, while winter-grazed treatments were much more grassy. Similar results were found later at the Seligman Old Block trials (Roux, 1990; O'Connor and Roux, 1995) and elsewhere (Tidmarsh, 1951), across a range of sites and soil types. The influence of seasonal grazing is understood better for grasses than for dwarf shrubs. Karoo grasses are predominantly C_4, growing best during warm weather, and slowly in cold weather. Therefore, grasses grazed during summer are being grazed at the only time of year when they actively grow, have photosynthetic material repeatedly removed, which is damaging to them, and populations decline as a consequence (Roux, 1966; Roux and Vorster, 1983a). By contrast, grasses grazed in winter are generally not growing, and leaves may have died and become photosynthetically inactive (Danckwerts, 1989), and therefore they are unlikely to be strongly negatively affected. An exception is the mat-forming grass *Tragus koelerioides* which has a decumbent growth form and can avoid and hence survive summer grazing (Roux, 1991). Shrub growth is more complex, being a function of a complex relationship between grazing, soil type, water-availability, temperature, and phenological state (Tidmarsh, 1951; du Preez, 1971; Cowling and Roux, 1987). Repeated summer grazing can induce a shift from grassy Karoo to pure shrubland through the extirpation of grasses rather than an increase in shrubs, while repeated winter grazing can reduce shrub populations (Roux, 1964; Vorster *et al.*, 1983). Following the response of grasses to summer grazing, it would be expected that palatable shrubs would be suppressed under the same conditions, while unpalatable shrubs would increase. The latter is often true, for example the highly unpalatable *Chrysocoma ciliata* can flourish under summer grazing, but palatable shrubs, e.g. *Phymaspermum parvifolium* (Roux, 1990) and *Pentzia incana* (Roux, 1965a) can also, though there may be a general inverse relationship between the abundance of palatable and unpalatable shrubs (Roux, 1965b).

The purpose of this study was to test the thesis that season of grazing is a primary determinant of vegetation composition and the abundance of various growth forms and species, and that recent rainfall (past 3 years) as well as long-term trends in rainfall further modify composition and abundance.

The hypotheses that were addressed were:

1. Botanical composition of perennial species is influenced by season of grazing, recent rainfall, and long-term trends in rainfall;
2. Abundance of individual growth forms, and species of grasses and perennial shrubs, are related to season of grazing, recent rainfall, and long-term trends in rainfall.

4.2 Methods

4.2.1 Study site

This study took place at the Grootfontein Agricultural Development Institute (31.4717°S, 25.0260°E), which partially encircles the town of Middelburg in the Eastern Cape Province, South Africa. At the time of the surveys reported on here (1949-1967) , the vegetation was classified as False Upper Karoo (Acocks, 1953), and more recently as the Eastern Upper Karoo (Vegetation Type: NKu4) (Mucina, Rutherford, *et al.*, 2006). Vegetation is grassy dwarf shrubland comprising numerous growth forms, the most common perennial forms being tufted grasses, non-succulent dwarf shrubs, succulent dwarf shrubs, stoloniferous grasses, and geophytes (du Toit *et al*. 2014). Annual and biennial grasses and various ephemeral species irrupt following rains (O'Connor and Roux, 1995). Mean annual precipitation at the time (1889-1969) was 355 mm. Approximately 75% of the rain falls from October to March, and 25% from April to September (du Toit and O'Connor, 2014). Growth of plants, and C_4 grasses in particular, is limited by rainfall and by the long frost season which occurs on average from mid-April to mid-October (du Toit and O'Connor, 2016b). Data were collected at two sites, the Camp 6 and the Seligman trials, which lie approximately 1.4 km apart (Figure 4.1).

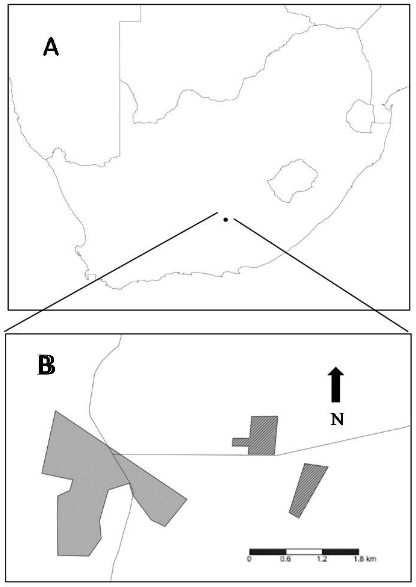


Figure 4.1. Location of Grootfontein in South Africa (A) and the locations of Middelburg (left shaded), and the Camp 6 (upper right shaded) and Seligman (lower right shaded) grazing trials (B).

4.2.2 Trials and Treatments

The Camp 6 trials were initiated in 1934. They are situated on gently-sloping land (<3°) predominantly of loam soils (Roux, 1993). The Seligman trials lie on slightly flatter land, and the upper section has loam soils and the lower section brackish soils (Roux, 1990). The Camp 6 treatments focused primarily on season of grazing, while those at Seligman also focused on various types of rotational grazing (Tidmarsh, 1951). Treatments selected for this study were those that had remained unchanged since the commencement of the trials, had treatments where the proportion of grazing occurring over the long-term in Summer (October – March) and Winter (April – September) could be defined (Table 4.1), and which were stocked at the same long-term stocking rate (1 LSU per 9 ha). The summer/ winter dichotomy was chosen for simplicity, though the intensity of grazing within each of these two seasons is not defined. For example, 100% summer grazing could refer to grazing from October to March, or grazing from November to February. This variation is recognised when interpreting results.

4.2.3 Data and statistical analysis

Monthly rainfall data were obtained from a weather station at Grootfontein, approximately 4.5 km to the west. Vegetation data came from surveys conducted from 1949 to 1967 (Table 4.1), and the response variable was percentage basal cover estimated using the wheel-point method of Tidmarsh and Havenga (1955). Nomenclature follows Germishuizen and Meyer (2003).

All composition data (perennial) were analysed using Canonical Correspondence Analysis (CCA) using the CANOCO 4.5 package (Ter Braak and Šmilauer, 2002) to identify the environmental effects of site location and soil type on composition and identify significantly different sites. Data from 1) Camp 6, 2) Seligman loam soil (Seligman loam) and 3) Seligman brackish soil (Seligman brackish) were then analysed separately using CCA to examine the effects of proportion of grazing occurring in the summer (Summer), the average of the past three seasons' rainfall (Rain) and time (Year) on vegetation composition.

The response of species and various growth forms to Summer, Rain (1-year rainfall for short-lived species; 3-year average rainfall for other species), and Year were explored using a General Linear Model (GLM). Interactions of Summer with Year and of Rain with Year were included to test for the cumulative effects of summer grazing and rainfall over time, but were then excluded from the model if non-significant. Type I sum of squares was used to measure the contribution of each variable to the model in the order they are added. Variables were fitted in the order of Summer, Rain, Time, and the interaction of Summer with Year and of Rain with Year.

Patterns of change of the relative abundance of the two major growth forms (perennial dwarf shrubs and perennial grasses) at each of the three sites were examined graphically in relation to the Standardised Precipitation Index (World Meteorological Organization 2012).

Table 4.1. Details of treatments at the Camp 6 and Seligman Old Block sites included in this study

Site and soil type	**Camp name**	**Grazing details**	**Years surveyed**
Camp 6 loam	1A	Sep – Feb every year (83% summer, 17% winter)	1950 1951 1952 1954 1959 1960 1961 1963 1965 1966 (5T not surveyed in 1950 and 1951)
	1B	Mar – Aug every year (17% summer, 83% winter)	
	2B	Year-long (continuous) grazing (50% summer, 50% winter)	
	3A	Sep – Dec every year (75% summer grazing, 25% winter grazing)	
	3B	Jan – Apr every year (75% summer, 25% winter)	
	3C	May – Aug every year (0% summer, 100% winter)	
	5T	Year-long (continuous) every year (50% summer, 50% winter)	
Seligman brackish	2	Rotational stocking such that each paddock grazed once each in spring (Sep-Oct), summer (Nov-Mar), autumn (Mar-Apr) every 3 years (spring and autumn in the same year) (50% summer, 50% winter)	1949 1950 1951 1954 1956 1958 1960 1961 1963 1965 1967
	3		
	4		
	A	Sep – Oct every year (50% summer, 50% winter)	
	B	Nov – Feb every year (100% summer, 0% winter)	
	C	Mar – Apr every year (50% summer, 50% winter)	
	D	May – Sep every year (0% summer, 100% winter)	
Seligman loam	11	Year-long (continuous) every year (50% summer, 50% winter)	
	12	Sept – Oct and Mar – Apr every year (50% summer, 50% winter)	
	13	Nov – Feb every year (100% summer, 0% winter)	
	14	May – Aug every year (0% summer, 100% winter)	

4.3 Results

4.3.1 Rainfall

Average rainfall over the study period (1949-1967 inclusive) was 353 mm, very close to the average over the past 50 years (351 mm). There was a minimum seasonal rainfall of 219 mm (1948/1949) and a maximum seasonal rainfall of 454 mm (1962/1963). The driest 6-month period was from June to November 1962 (15.7 mm), the driest 12-month period was from December 1967 to November 1968 (148.6 mm), and the driest 18-month period was from June 1967 to November 1968 (206.5 mm). Approximately equal numbers of years over the study period were above average and below average rainfall.

Rainfall decreased significantly over the duration of the study at a rate of approximately 6 mm per year, or 120 mm over 20 years, although there was considerable variation ($F_{1,18}$=4.98, P=0.039, R^2=21.7%) (Figure 4.2). Accordingly, the factor Year is correlated with a linear decline in rainfall. Twelve-month Standardised Precipitation Index (SPI) values indicated periods of Extreme and Severe dryness toward the beginning and the end of the study, while Moderately Dry periods were common. Thirty-six month SPI values indicated normal rainfall conditions for most of the duration of the study, with some Moderately Dry conditions toward the end (Figure 4.2).

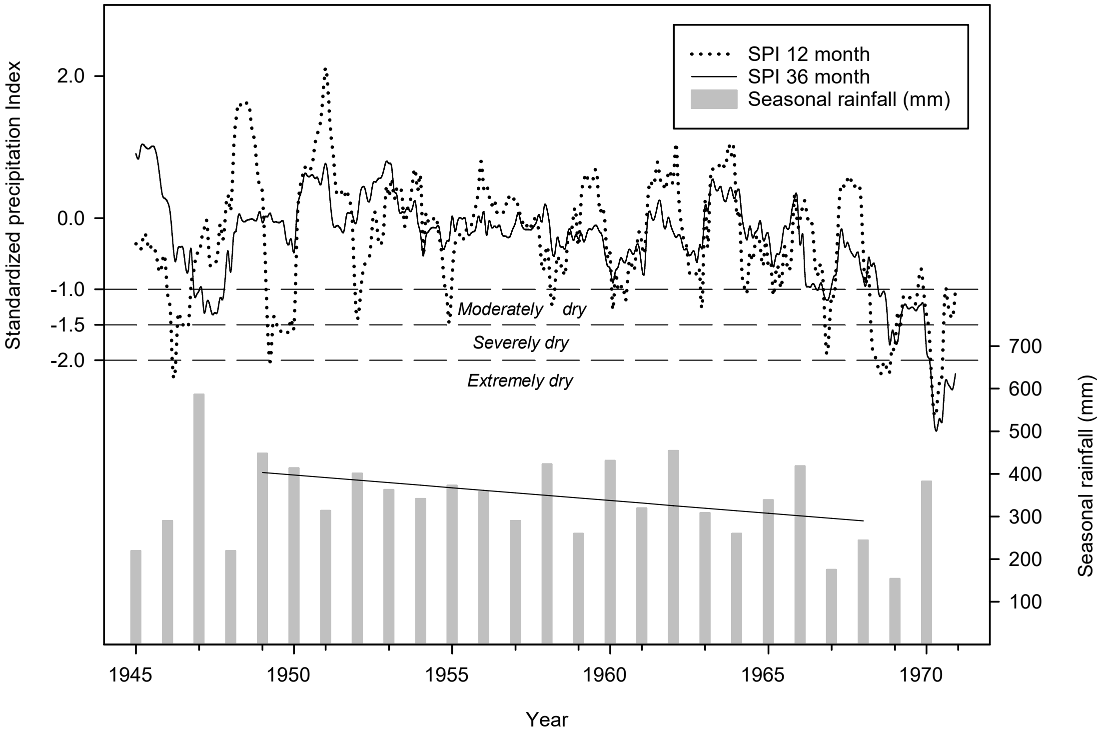


Figure 4.2 Rainfall at Grootfontein from 1945-1970 (bars) showing significant downward trend over the duration of the study (black line, $F_{1,18}$=4.98, P=0.039, R^2=21.7%) *and* expressed as Standardised Precipitation Index for 12-month and 36-month periods, highlighting periods of increasing dryness.

4.3.2 Vegetation - overview

Nine perennial and three short-lived growth forms, as well as trace numbers of unclassified genera, were encountered at the sites (Table 4.2). Eighty-six perennial species were found, of which most were dwarf shrubs (41), grasses (20), and herbs (10). Short-lived species were predominantly herbs (13) and grasses (5). The most abundant dwarf shrubs were *Chrysocoma ciliata* and *Pentzia incana*, while grasses were *Eragrostis lehmanniana* and *Tragus koelerioides*. The only relatively common perennial herb was *Salvia verbenaca* (an exotic), and the only common short-lived species (19 in total) was the grass *Aristida congesta*.

Table 4.2. Average basal cover of all species per paddock over the duration of the study, according to growth form, for Camp 6 (C6), Seligman loam (SL) and Seligman brackish (SB) sites. Values follow a logarithmic scale of basal cover (b), where 5 = b≥1%, 4 = 1%>b≥0.1%, 3=0.1%>b≥0.01%, 2=0.01%>b≥0.001% and 1=0.001%>b≥0.0001%. Species highlighted in grey are those discussed in the text

Taxon	**Code**	**C6**	**SL**	**SB**
Perennial cyperoid herb				
Cyperus usitatus	Cypusi	3	2	2
Perennial herb				
Aptosimum procumbens	Aptpro	3	2	3
Arctotheca populifolia	Arcpop		2	2
Berkheya rigida	Berrig	3	2	2
Dimorphotheca zeyheri	Dimzeh			2
Erigeron filifolius	Erifil	1		
Gazania jurineifolia	Gazjur		2	2
Gazania krebsiana	Gazkre	2		
Indigofera alternans	Indalt	3		2
Salvia verbenaca	Salver	4	3	2
Vellereophyton dealbatum	Veldea	1	2	2
Perennial herb geophyte				
Cyperus spp	Cypspp		2	2
Moraea spp	Morspp		2	
Oxalis depressa	Oxadep	3	3	3
Perennial dwarf shrub				
Amphiglossa triflora	Amptri	3	2	2
Berkheya annectens	Berann	2		2
Blepharis mitrata	Blemit	3	3	3
Chrysocoma ciliata	Chrcil	4	4	4
Eriocephalus ericoides	Erieri	3	3	4
Eriocephalus spinescens	Erispi	3	3	3
Felicia filifolia	Felfil	2	3	2
Felicia muricata	Felmur	3	3	3
Galenia procumbens	Galpro	2		
Galenia sarcophylla	Galsar		2	2
Gnidia polycephala	Gnipol	3	2	1
Helichrysum dregeanum	Heldre	2		4
Helichrysum lucilioides	Helluc	2	2	2
Helichrysum niveum	Helniv			2
Helichrysum rutilans	Helrut	3	2	1
Helichrysum zeyheri	Helzey	2		2
Hermannia linearifolia	Herlin		2	1
Jamesbrittenia atropurpurea	Jamatr			2
Jamesbrittenia filicaulis	Jamfil			2
Limeum aethiopicum	Limaet			2
Nenax microphylla	Nenmic	3	2	3
Osteospermum leptolobum	Ostlep	2	3	3
Pegolettia retrofracta	Pegret	1		
Pentzia globosa	Penglo	2		3
Pentzia incana	Peninc	4	5	4
Pentzia lanata	Penlan	2		
Pentzia sphaerocephala	Pensph			2

Taxon	**Code**	**C6**	**SL**	**SB**
Pentzia spinescens	Penspi	2		1
Phymaspermum parvifolium	Phypar	4	3	4
Plinthus karooicus	Plikar	2	3	3
Pteronia glauca	Ptegla	4	3	3
Pteronia glomerata	Pteglo	3	3	2
Pteronia sordida	Ptesor	3	2	
Pteronia tricephala	Ptetri	2	2	1
Rosenia humilis	Roshum	3	3	3
Salsola calluna	Salcal	3	3	2
Selago geniculata	Selgen	2	3	2
Selago saxatilis	Selsax	3	2	3
Stachys linearis	Stalin	3	2	2
Stachys rugosa	Starug		2	
Wahlenbergia tenella	Wahten	1	2	2
Perennial parasitic dwarf shrub				
Thesium hystrix	Thehys	3	3	3
Perennial succulent dwarf shrub				
Hertia pallens	Herpal	2		
Ruschia intricata	Rusint	2	2	
Ruschia spinosa	Russpi	3		4
Perennial succulent				
Aloe broomii	Alobro			1
Mestoklema tuberosum	Mestub	1		
Trichodiadema pomeridianum	Tripom	2	2	1
Perennial grass				
Aristida diffusa	Aridif	4	4	4
Cynodon incompletus	Cyninc	4	2	2
Digitaria argyrograpta	Digarg	2		
Enneapogon scoparius	Ennsco	2	3	2
Eragrostis bergiana	Eraber	3	3	2
Eragrostis bicolor	Erabic	3		
Eragrostis chloromelas	Erachl	2	2	2
Eragrostis curvula	Eracur	2	2	2
Eragrostis lehmanniana	Eraleh	5	4	5
Eragrostis obtusa	Eraobt	3	4	4
Fingerhuthia africana	Finafr		3	1
Heteropogon contortus	Hetcon			2
Oropetium capense	Orocap	3	3	3
Sporobolus fimbriatus	Spofim	2	2	3
Sporobolus ioclados	Spoioc			1
Sporobolus ludwigii	Spolud	2	3	3
Sporobolus tenellus	Spoten		2	
Stipagrostis obtusa	Stiobt	3		
Themeda triandra	Thetri	1		
Tragus koelerioides	Trakoe	5	4	4

Taxon	**Code**	**C6**	**SL**	**SB**
Perennial shrub				
Asparagus spp	Aspspp	2	2	2
Euryops spp	Eurspp		2	
Exomis microphylla	Exomic		2	
Lycium spp	Lycspp	4	4	4
Short-lived cyperoid herb				
Bulbostylis humilis	Bulhum	3	2	3
Short-lived herb				
Arctotheca calendula	Arccal	3		
Argemone mexicana	Argmex	1		2
Euphorbia prostrata	Euppro	2		
Geigeria filifolia	Geifil	2	2	2
Hermannia coccocarpa	Hercoc	2	2	2
Herniaria hirsuta	Herhis	2	2	
Ifloga glomerata	Iflglo	3	3	3
Lasiopogon glomerulatus	Lasglo		2	
Lepidium africanum	Lepafr	2		2
Medicago laciniata	Medlac	2	3	2
Trichogyne paronychioides	Tripar	3	3	3
Ursinia nana	Ursnan	2	2	3
Wahlenbergia androsacea	Wahand	2	2	2
Short-lived grasses				
Aristida congesta	Aricon	5	5	5
Chloris virgata	Chlvir	4	2	2
Enneapogon desvauxii	Enndes	3	3	2
Schismus barbatus	Schbar	2	2	2
Tragus racemosus	Trarac	3	3	3
Unclassified genera				
Amaranthus spp	Amaspp	1		
Crassula spp	Craspp	3	2	
Euphorbia spp	Eupspp	1		
Galenia spp	Galspp	2		1
Gazania spp	Gazspp	2		2
Ruschia spp	Russpp			2
Selago spp	Selspp			2
Sutera spp	Sutspp	1		

4.3.3 Vegetation – multivariate analysis

Canonical Correspondence Analysis (CCA) accounted for only 12.8% of the species variance (Table 4.3), but demonstrated that Site and Soil had a significant effect on both the first axis and on the overall ordination (Table 4.4). Both Site and Soil contributed significantly to the model. The ordination clearly demarcated Camp 6 loam soils, Seligman loam soils, and Seligman brackish soils (Figure 4.3), with very little overlap between sites. Camp 6 was strongly associated with the creeping grasses *Cynodon incompletus* and *Tragus koelerioides*, Seligman loam with the shrub *Pentzia incana* and grass *Enneapogon scoparius*, and Seligman brackish with the shrub *Eriocephalus ericoides*.

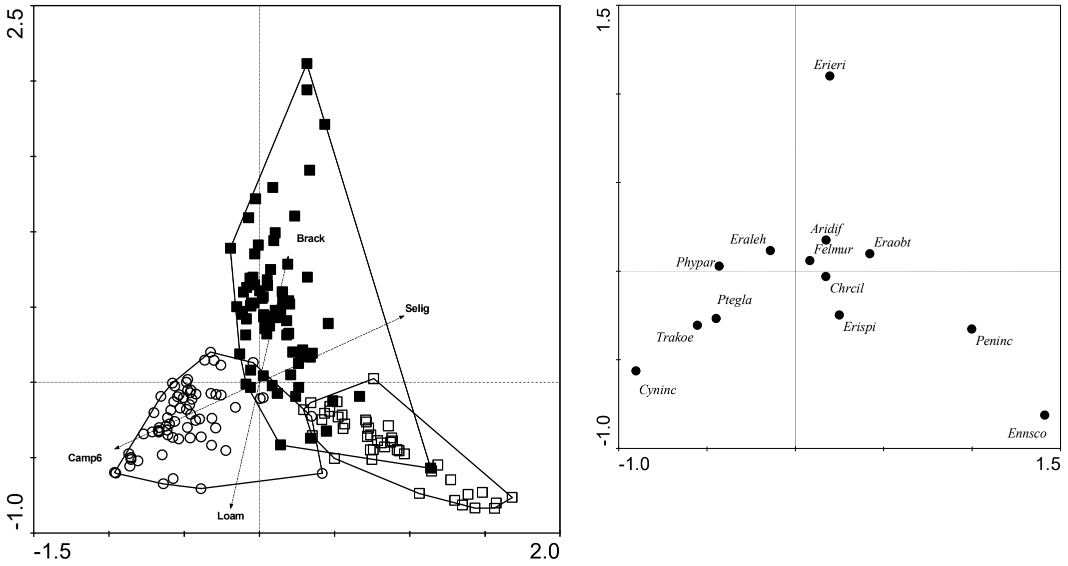


Figure 4.3 A plot x environment biplot (left) and species plot (right) of the Canonical Correspondence Analysis of all perennial plants grouped according to site and soil type (Camp 6 (loams) = open circles, Seligman (loams) = open squares, Seligman (brackish soils) = solid squares. Arrows are environmental variables. (See Table 4.2 for species codes).

For the Camp 6, Seligman loam and Seligman brackish sites, the CCA showed that environmental factors had significant effects on both the first axis and the overall ordination (Table 4.4). For all three sites, Year and Season contributed significantly to the model, and Rainfall did not. Variance in species accounted for was higher at the Seligman loam sites (approximately 20%) than at the Seligman brackish site (7%).

Table 4.3 Summary statistics of Canonical Correspondence Analyses

	All		Camp 6		Selig loam		Selig brackish	
	Ax1	Ax2	Ax1	Ax2	Ax1	Ax2	Ax1	Ax2
Eigenvalues	0.255	0.145	0.182	0.168	0.239	0.086	0.096	0.067
Species-environment correlation	0.897	0.781	0.894	0.790	0.910	0.824	0.703	0.771
Cumulative percentage variance								
Species data	8.2	12.8	9.9	19.0	14.5	19.7	4.0	6.8
Species-environment correlation	63.8	100	47.5	91.4	69.1	93.8	53.8	91.3

Table 4.4 Test statistics for first and all axes, and for environmental variables based on Monte-Carlo permutation tests (499 permutations)

	All		Camp 6		Selig loam		Selig brackish	
	F-ratio	P-value	F-ratio	P-value	F-ratio	P-value	F-ratio	P-value
Test of significance of canonical axes								
First	16.51	0.002	7.004	0.002	6.779	0.002	3.071	0.002
All	13.63	0.002	5.589	0.002	3.539	0.002	1.973	0.002
Canonical coefficients								
Site	14.5	0.002						
Soil	11.91	0.002						
Year			7.15	0.002	2.64	0.002	2.38	0.006
Season			7.35	0.002	7.02	0.002	2.97	0.002
Rainfall			1.47	0.070	0.74	0.714	0.65	0.886

The first axis of the CCA for Camp 6 completely separated the early (1950-1954) data from the late (1959-1966) data (Figure 4.4). On the second CCA axis, sites were arranged in a gradient from summer grazing to winter grazing, with the sites receiving predominantly winter grazing separating from the other sites during the late period. Winter grazing was associated with the perennial grasses *Eragrostis lehmanniana* and *Aristida diffusa*, and summer grazing with the shrub species *Phymaspermum parvifolium*, *Pentzia incana*, *Chrysocoma ciliata,* and *Pteronia glauca*. The creeping grass *Cynodon incompletus* was associated with the early period, and declined to 15% of its relative abundance by the late period. The other common creeping grass, *Tragus koelerioides*, showed the opposite effect and increased to 330% of its relative abundance over time.

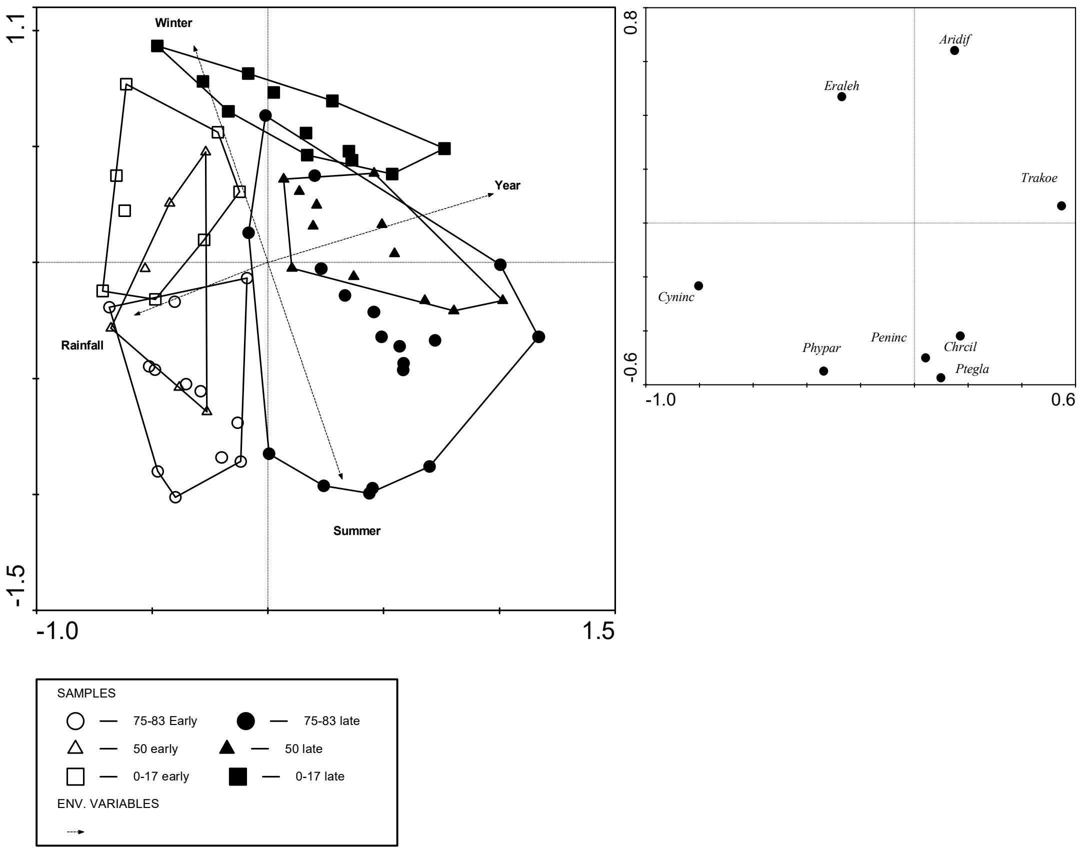


Figure 4.4 A plot x environment biplot (left) and species plot (right) of the Canonical Correspondence Analysis of all perennial plants at Camp 6 grouped according to proportion of grazing during summer (squares, triangles and circles in decreasing order) for early (1950-1954; open markers) and late (1959-1966; solid markers) periods. Arrows are environmental variables. (See Table 4.2 for species codes).

At Seligman loam, the first axis of the CCA showed a trend from winter to summer grazing, and the second axis change over time, with clear separation between the various groups (Figure 4.5). Winter grazing was associated with the grass species *Enneapogon scoparius*, *Eragrostis obtusa*, *Aristida diffusa*, and *Eragrostis lehmanniana*, while summer grazing was associated with the shrub species *Pentzia incana* and *Chrysocoma ciliata*. *Enneapogon scoparius* increased by 50% from the early (1949-1958) to the late (1960-1967) period, but only in the treatments that were not grazed only in summer.

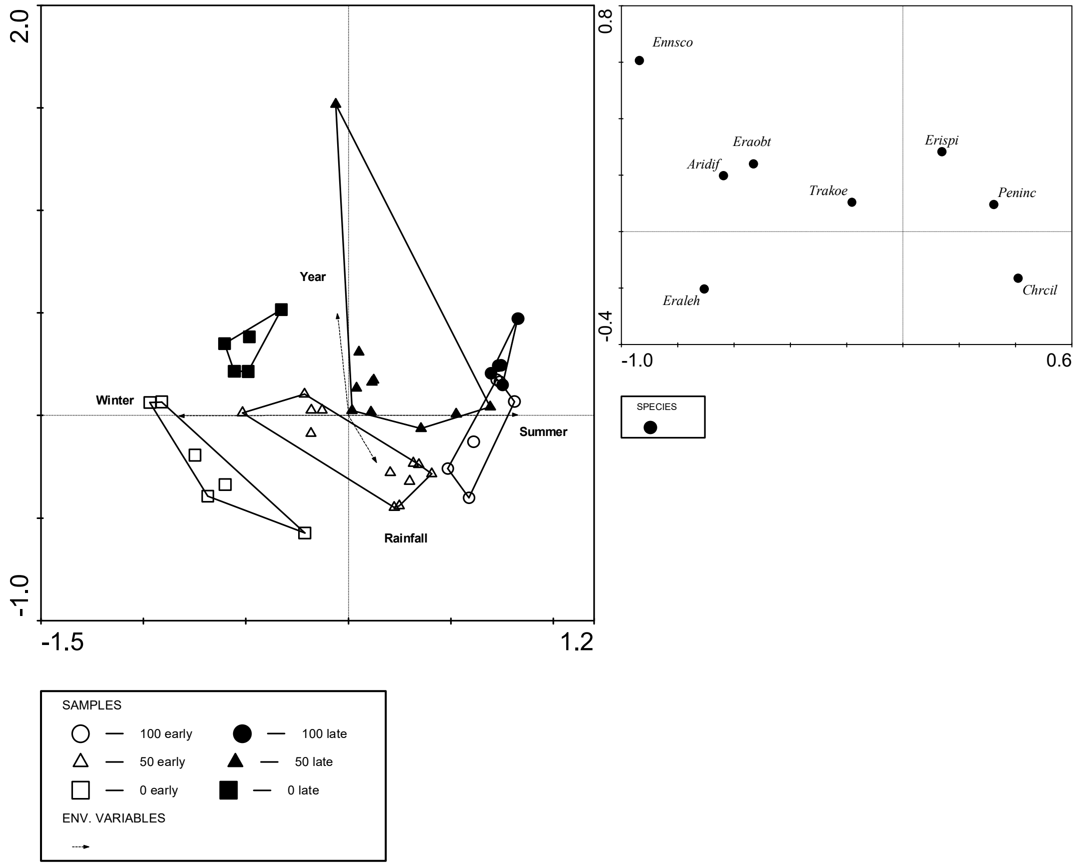


Figure 4.5 A plot x environment biplot (left) and species plot (right) of the Canonical Correspondence Analysis of all perennial plants at Seligman loam grouped according to proportion of grazing during summer (squares, triangles and circles in decreasing order) for early (1949-58; solid markers) and late (1960-1969; open markers) periods. Arrows are environmental variables. (See Table 4.2 for species codes).

At the Seligman brackish site, the first CCA axis was principally a summer/winter gradient, and the second axis related to time (Figure 4.6). Sites that were grazed only in summer were clearly distinct from all other sites. Winter grazing was associated with the grasses *Eragrostis obtusa* and *Eragrostis lehmanniana*, and the shrub *Eriocephalus ericoides* increased to 198% of its early abundance over time in the summer-only treatments, but increased only slightly (by 19%) in the other treatments. *Tragus koelerioides* also increased from the early to late periods by 100% in treatments that had some winter grazing, while in the summer-only grazed treatment it declined over time to 24% of its previous levels. *Phymaspermum parviflorum* showed a similar decline (to 23%) across all treatments.

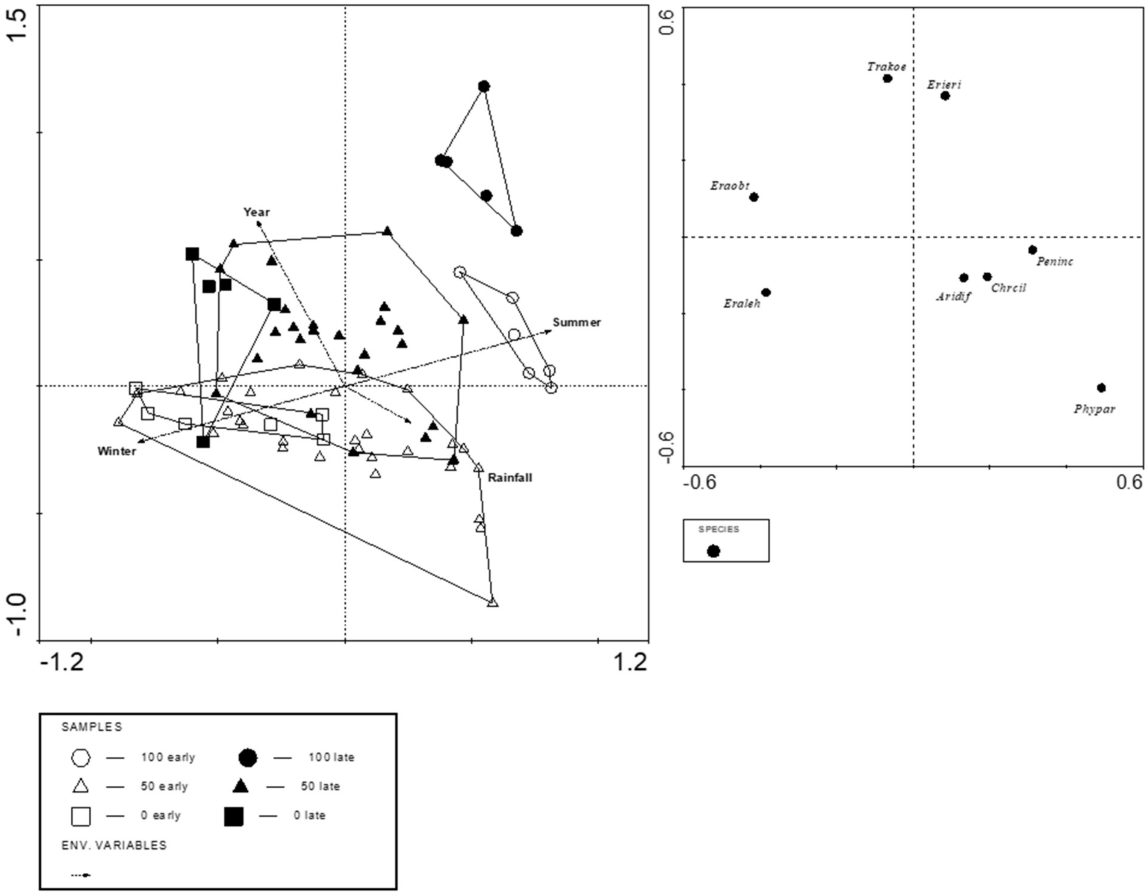


Figure 4.6 A plot x environment biplot (left) and species plot (right) of all perennial plants at Seligman brackish grouped according to proportion of grazing during summer (squares, triangles and circles in decreasing order) for early (1949-58; solid markers) and late (1960-1969; open markers) periods. Arrows are environmental variables. (See Table 4.2 for species codes).

4.3.4 Vegetation – univariate analysis

In all analyses, the interactions of Summer*Year and Rain*Year were not significant and were removed, and statistics are not presented here. General Linear Models (GLM) revealed that the variables Summer, Rainfall and Year explained significant amounts of variation in basal cover of the various taxa and species (Table 4.5). The group of all perennial shrubs plus perennial grasses (Perennials) was negatively related to summer grazing, and declined over time. Short-lived grasses were highly responsive to the past year's rainfall, responded negatively to summer grazing, and declined over time. Perennial shrubs showed a similar response to 3-year rainfall, but the magnitude of the effect was smaller. Perennial grasses were negatively related only, and strongly, to summer grazing. Palatable and unpalatable shrubs both responded positively to summer grazing and both declined in abundance over time. Palatable shrubs showed a weak positive relation to rainfall, and unpalatable shrubs a very weak negative relation. The shrubs *Chrysocoma ciliata* (unpalatable), *Pentzia incana* and *Phymaspermum parvifolium* (both palatable) all responded positively to summer grazing and all declined over time; *P. parviflorum* also responded positively to increased rainfall. The short-lived grass *Aristida congesta* responded in the same way as short-lived grasses in general. Perennial grass species were noticeably different in their response to summer grazing, rain, and time. *Aristida diffusa* responded negatively to summer grazing. *Eragrostis lehmanniana* also responded negatively to summer grazing, declined over time, and showed a positive response to rainfall. *Tragus koelerioides* increased strongly over time, but was not related to summer grazing or to rainfall.

Table 4.5. Results from fitting General Linear Models to the abundance (basal cover) of various plant growth forms and species at Grootfontein

Analysis of variance

Growth form/ species	**Df**	**F-ratio**	**P-value**	**R^2**
Perennial shrubs + grasses	3,185	15.17	<0.0001	19.74
Short-lived grasses	3,185	31.93	<0.0001	34.12
Perennial shrubs	3,185	29.44	<0.0001	32.31
Perennial grasses	3,185	33.15	<0.0001	34.96
Palatable dwarf shrubs	3,185	14.56	<0.0001	19.10
Unpalatable dwarf shrubs	3,185	16.06	<0.0001	20.66
Chrysocoma ciliata	3,185	10.21	<0.0001	14.21
Pentzia incana	3,185	4.71	0.0034	7.11
Phymaspermum parviflorum	3,185	20.36	<0.0001	24.82
Aristida congesta	3,185	35.26	<0.0001	36.38
Eragrostis lehmanniana	3,185	55.59	<0.0001	47.41
Tragus koelerioides	3,185	4.42	0.005	6.68
Aristida diffusa	3,185	14.34	<0.0001	18.86

Parameter estimates

Growth form/ species	**Source**	**F-ratio**	**P-value**	**Estimate (x1000)**
Perennial dwarf shrubs + grasses	Summer	24.1	<0.0001	-4.4
	Rainfall	2.91	0.0897	
	Year	18.49	<0.0001	-22.0
Short-lived grasses	Summer	13.08	0.0004	-12.8
	Rainfall	56.53	<0.0001	10.1
	Year	26.19	<0.0001	-94.3
Perennial dwarf shrubs	Summer	42.66	<0.0001	5.6
	Rainfall	10.9	0.0012	0.3
	Year	34.77	<0.0001	-29.3
Perennial grasses	Summer	97.35	<0.0001	-13.5
	Rainfall	0.13	0.723	
	Year	1.97	0.1626	

Palatable dwarf shrubs	Summer	17.43	<0.0001	3.8
	Rainfall	7.99	0.0052	0.6
	Year	18.27	<0.0001	-22.6
Unpalatable dwarf shrubs	Summer	26.56	<0.0001	4.3
	Rainfall	4.34	0.0387	-0.0
	Year	17.28	<0.0001	-20.4
Chrysocoma ciliata	Summer	21.36	<0.0001	11.3
	Rainfall	0.30	0.5865	
	Year	8.97	0.0031	-42.9
Pentzia incana	Summer	4.17	0.0427	5.9
	Rainfall	1.86	0.1748	
	Year	8.12	0.0049	-48.1
Phymaspermum parviflorum	Summer	10.78	0.0012	7.5
	Rainfall	16.64	0.0001	2.7
	Year	33.64	<0.0001	-76.8
Aristida congesta	Summer	12.86	0.0004	-11.1
	Rainfall	48.34	<0.0001	8.1
	Year	44.57	<0.0001	-107.4
Aristida diffusa	Summer	42.5	<0.0001	-17.8
	Rainfall	0.01	0.9401	
	Year	0.50	0.4808	
Eragrostis lehmanniana	Summer	147.45	<0.0001	-32.1
	Rainfall	5.37	0.0215	1.2
	Year	13.93	0.0003	-57.5
Tragus koelerioides	Summer	2.59	0.1089	
	Rainfall	0.43	0.5145	
	Year	10.23	0.0016	52.9

4.3.5 Temporal changes of dwarf shrubs and grasses

The abundance of dwarf shrubs declined significantly over time (Table 4.5), and this occurred abruptly during the early 1950s (Figure 4.7), and populations remained low for approximately a decade then showed some increase. At the same time grass abundance at Camp 6 collapsed dramatically, but then recovered quickly. Grass abundance at the Seligman sites was not recorded during this time, but tracked Camp 6 populations from 1954 to 1960. Conditions had been Extremely Dry several years earlier (until Jan 1950) followed by a period of wet conditions until mid-1951. There was a brief drought during the summer of 1951/52, followed by generally good rainfall for several years. Collapse and recovery of populations of dwarf shrubs were generally similar at all three sites, and largely unrelated to summer grazing (Figure 4.8), although there had been a flush of *Phymaspermum parviflorum* at one site at Camp 6 (Figure 4.8A). Grass recovery at Camp 6 was generally quick, but there was a near-complete collapse of grasses in the summer-grazed treatment after 1960 (Figure 4.8B). Grass populations in the summer-grazed treatments at the Seligman sites collapsed in the mid-1950s and remained low for the remainder of the study (Figure 4.8D and F)

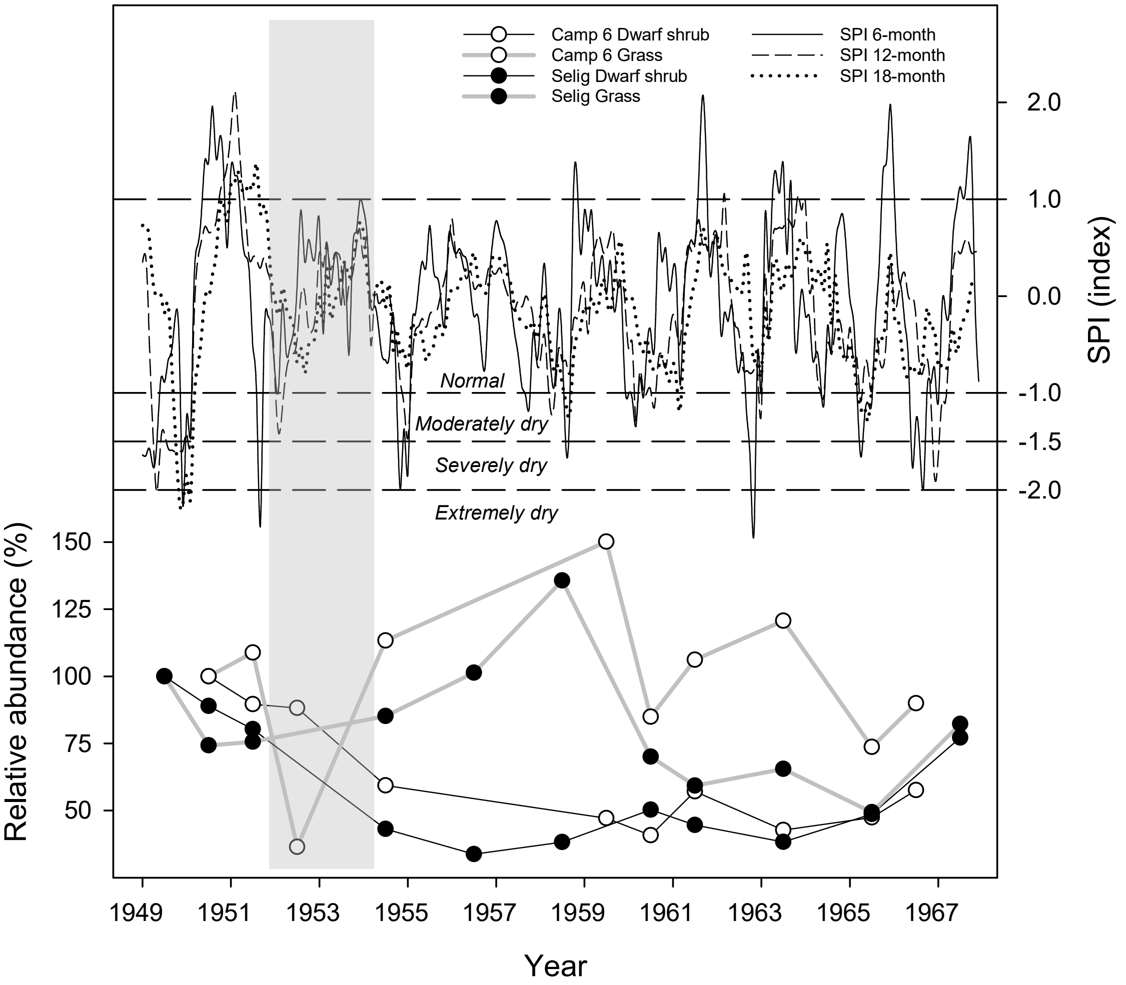


Figure 4.7. Standardised Precipitation Index (SPI) for 6-, 12-, and 18-month periods and relative abundance of grasses and shrubs at the Camp 6 and Seligman sites. The grey block highlights the time period during which there was severe mortality of shrubs and grasses.

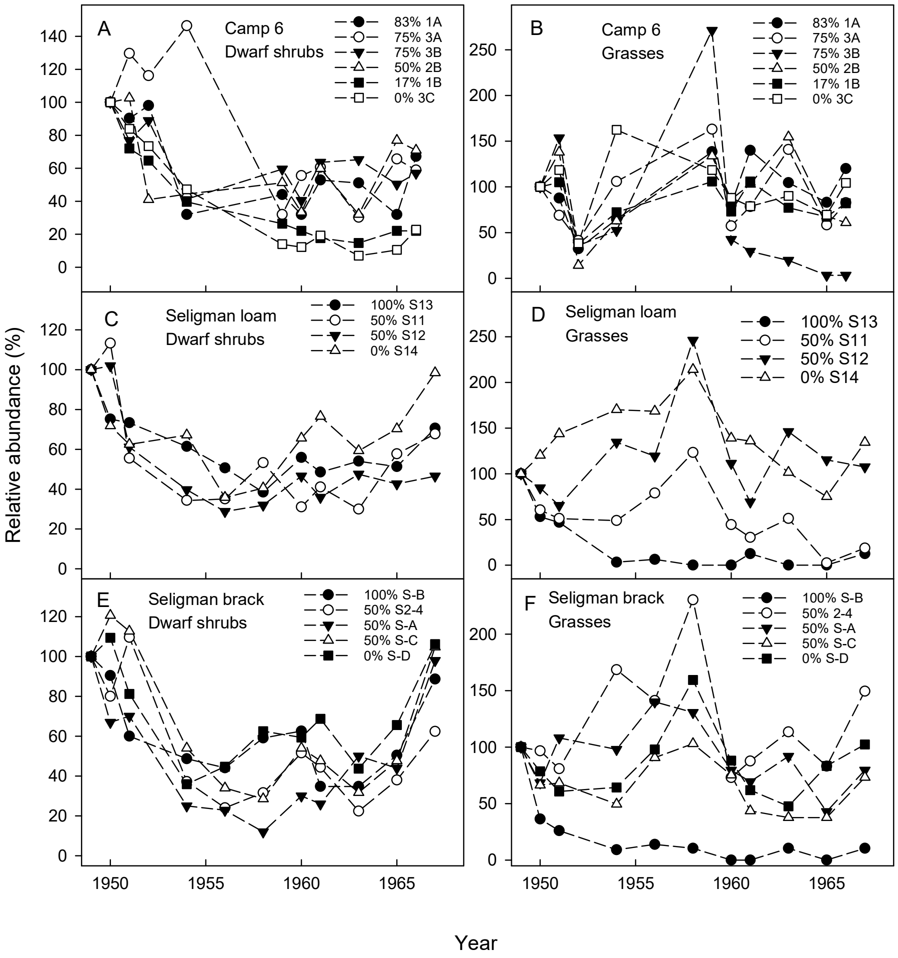


Figure 4.8. Changes in abundance of grasses (B, D and F) and dwarf shrubs (A, C and E) at three sites at Grootfontein, relative to that in 1949. See Table 4.2 for explanation of percentages and codes in the legends.

4.4 Discussion

Rainfall during the study period varied as expected in a semi-arid environment, but also showed a general decline over time. Variation prior to the study period was higher, with some Severely Dry periods and some very wet periods. Dry periods were, however, only evident at a 12-month scale, while at a 3-year scale conditions were generally ‘normal’. These patterns might be predictive of occasional collapses in grass populations (O’Connor and Roux, 1995) but not in shrub populations, these being more drought-tolerant (Midgley and van der Heyden, 1999). The general downward trend in rainfall would suggest an overall decrease in plant cover.

The directional changes in composition at Camp 6 in large part reflect the changes observed for two perennial creeping grass species, *Cynodon incompletus* which does not tolerate drought (Novellie and Bezuidenhout, 1994), and the more drought-resistant *Tragus koelerioides* (Roux, 1967b). Predominantly summer-grazed sites showed considerable variation in composition, possibly owing to differences in timing of grazing across the treatments and the inter-annual fluctuations in *Eragrostis lehmanniana*, a perennial species that responds relatively quickly to rain (Roux, 1973). Summer grazing strongly influenced the abundance of several shrub species which differed markedly in palatability. *Chrysocoma ciliata* is very unpalatable, while *Phymaspermum parviflorum* and *Pentzia incana* are palatable, and all increased with summer grazing. This highlights a fundamental difference in response between grass and dwarf shrub growth forms in terms of survival if not growth rate or productivity, although *Tragus koelerioides* appears to be an exception. Winter-grazed sites varied less, and showed lower compositional variation during the late than the early period, and were associated with grass species. Composition at the Seligman loam and brackish sites generally mimicked that of the Camp 6 site, although the delineation of sites was clearer at Seligman loam, and there were differences in dominant species. At the Seligman brackish site the shrub *Eriocephalus ericoides* increased over time – this species often becomes locally dominant in the Karoo, despite not being particularly abundant at the study site.

Total cover of Perennials conformed to expectations, being inversely related to the degree of summer grazing, and decreasing over time with a decrease in rainfall. Not expected is that the perennial grass component did not decrease over time. This appears to be because *Aristida diffusa* managed to maintain its abundance, and *Tragus koelerioides* increased over time. *Aristida diffusa* is a large and generally unpalatable grass but even so declined in the presence of summer grazing. This indicates that its unpalatability is insufficient to repel sheep, but it appears to be drought-tolerant. Other *Aristida* species have shown similar responses in Australia (Clarkson and Lee, 1988). *Tragus koelerioides* is highly responsive to rainfall, and can swiftly occupy denuded areas following disturbance such as drought or fire (Novellie and Bezuidenhout, 1994; Snyman and Cowling, 2004). *Eragrostis lehmanniana* populations generally had a predictable response to summer grazing and decreasing rainfall trends, and the comparatively small positive correlation with rainfall is likely a result of its strong response to recent rainfall (Frasier and Cox, 1994) rather than rainfall over a three-year period. Short-lived and perennial grasses in general were significantly suppressed by summer grazing, with *Tragus* *koelerioides* being an exception. Abundance of this species was not related to summer grazing, presumably as it can escape herbivory owing to its growth form. Rates of increase or decrease of grass populations were not constant over time and showed marked fluctuations. At Camp 6 there was a severe collapse in 1952 followed by a swift recovery and then generally a slow decline in populations. The summer-grazed treatment (3B; grazed Jan-Apr) had a large flush of *Tragus koelerioides* in 1958, followed by a steep collapse of cover of all perennial grasses until the end of the trial. At the Seligman sites the summer-grazed sites similarly declined nearly to zero, though the collapse was evident by 1954. Thus with very intense grazing in the middle of summer, even *Tragus koelerioides* was unable to persist. It is unknown whether the 1952 grass collapse experienced at Camp 6 also occurred at the Seligman sites because vegetation was surveyed in 1951 and again only in 1954.

Abundance of shrubs was positively related to summer grazing, and this was more pronounced for the unpalatable *Chrysocoma ciliata* than for the palatable *Phymaspermum parvifolium* and *Pentzia incana*. This positive relation of both palatable and unpalatable shrubs to summer grazing suggests that, whatever the impact of summer grazing might be to palatable species, they flourish more than if grazed in winter. This could be a function of competition (Hoffman *et al.*, 1990), because in winter-grazed treatments grasses tend to proliferate, or possibly because some shrub species may change in palatability during the year, for example *Phymaspermum parvifolium* that during summer is hard and dry and is green and succulent during winter (Roux, 1990).

Both palatable and unpalatable shrubs decreased over time, while palatable shrubs also responded to rainfall mainly owing to increases in the population of *Phymaspermum parvifolium*. As with grasses, the rate of decrease of shrubs was not constant, though it was less variable. The general trend was a rapid decrease in shrub populations between 1951 and 1954, followed by a slow recovery over the next decade. Was this collapse due to rainfall? The approximately concomitant collapse in grass populations would suggest so, this seemingly having been caused by the Extremely Dry period the summer before. However, shrub populations at Camp 6 in 1952 hadn’t yet collapsed, though by 1954 had. Post-1952, however, rainfall was generally good. Additionally, an Extremely Dry period during the summer of 1962/63 was not associated with a large collapse in shrubs (though there was a small reduction), though it should be recognised that at this time populations were approximately only half that of pre-1952, so perhaps were better able to withstand drought. Despite the generally good rains measured after 1952, at the time it was certainly perceived that the country was experiencing a severe drought (Adler, 1953). Therefore, if drought does cause general collapses in shrub populations, the mechanism is more complex than can be explained merely by looking at recent rainfall amount. Precise timing (seasonality) of rainfall, temperature, and the phenological state of plants have been invoked (Roux, 1965a), and further analysis would be needed.

4.5 Conclusion

The following is concluded with respect to the two hypotheses presented earlier.

Hypothesis 1

Season of grazing and long-term rainfall trend strongly influence perennial vegetation composition, while 3-year rainfall has a negligible effect.

Hypothesis 2

Season of grazing was a potent determinant of grass cover for most grass species, and influenced shrub cover. Recent rainfall influenced mainly short- to medium-lived grasses. Long-term rainfall trend was associated strongly with cover of most growth forms and species, but the mechanisms of this remain unexplained.

CHAPTER 5 VEGETATION CHANGES AT THE BOESMANSKOP RESEARCH TRIALS, GROOTFONTEIN, 2007-2015

5.1 Introduction

The Nama-Karoo is a biome dominated by grasses and dwarf shrubs, with the proportion of grasses being positively correlated to both long-term and short-term rainfall (Mucina, Rutherford, *et al.*, 2006). Nama-Karoo eventually transitions into semi-arid grassland along its eastern boundary, though the influence of increased rainfall is confounded with changes in altitude and topography. Owing to fluctuations in rainfall amount and strong competitive advantage that high rainfall bestows on grasses, the position of the boundary between the Nama-Karoo and the Grassland Biomes has varied, moving east in times of high rainfall and west in times of low rainfall (Scott and Lee-Thorp, 2004; Mucina, Hoare, Lötter, *et al.*, 2006; Scott *et al.*, 2012).

Vegetation cover in the Nama-Karoo is influenced by various factors including rainfall, geology, soil type, and grazing history, but is almost always less than 100% (Milton and Hoffman, 1994; Keay-Bright and Boardman, 2006; Dreber *et al.*, 2011). Following dry periods, increased soil moisture availability typically results in a rapid flush of short-lived grass species (Bedford and Roberts, 1975; O'Connor and Roux, 1995), and it is anticipated that under prolonged conditions of high moisture availability perennial grasses will colonise gaps and increase in abundance (Milton and Hoffman, 1994; Smith, 2000) at the expense of annual grasses which will decline. Shrub species also germinate and colonise, but much less is known about their dynamics, though it is likely that their ingress into Karroid communities is much slower than with grasses (Cowling and Roux, 1987; Milton and Hoffman, 1994; Wiegand *et al.*, 1998).

Much of the Karoo experienced high rainfall conditions in recent decades, including at Grootfontein in the eastern Karoo (du Toit, 2010), including some very high rainfall years during the early 2010s (du Toit, 2015). These conditions offered an opportunity to examine the effects of multiple high rainfall years on the cover and composition of Nama-Karoo vegetation.

In particular, the following hypotheses were addressed regarding cover and composition of Karroid veld in times of high rainfall:

1. Total vegetation cover will increase;
2. Cover of annual or short-lived grasses will decline;
3. Cover of perennial grasses will increase; and
4. Cover of shrubs will increase but to a lesser extent than grasses.

5.2 Methods

5.2.1 Study site

This study was conducted at the Boesmanskop research trials that are located on the farm of the Grootfontein Agricultural Development Institute near Middelburg in the eastern Karoo. The area falls within the Eastern Upper Karoo of the Nama-Karoo Biome (Mucina, Rutherford, *et al.*, 2006). The Boesmanskop trials were established in 1989 to monitor the effect of recommended grazing systems using animals stocked at recommended rates on vegetation change over time (du Toit, 2001).

The trials comprise an area of land approximately 206 ha in extent which is divided into eleven paddocks (Figure 5.1). Eight of these are approximately 14 ha each and lie on the plains or pediments, and three paddocks are approximately 30 ha each and are situated on a low-lying hill. The trials are stocked with a single group of animals (six cattle and 36 sheep) that graze the smaller plains paddocks for two weeks and the larger hill paddocks for four weeks each on an ongoing rotation. The long-term stocking rate is approximately 16 hectares per animal unit, and the ratio of sheep:cattle is approximately 1:1 on a metabolic mass basis (Meissner, 1982).

Two unplanned fires occurred in the trials (not on the same place) in 1976 and in 2012. Details of the short-term response of the vegetation to the 2012 fire are described by du Toit *et al.*, (2014).

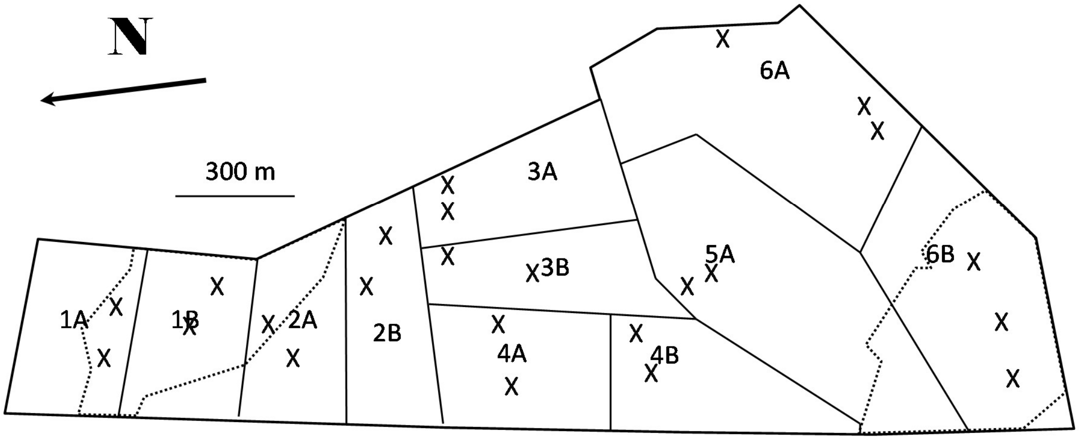


Figure 5.1 Layout of the Boesmanskop trials at Grootfontein. Dotted lines demarcate the approximate position of fires in 1976 (left) and 2012 (right). 'X' marks show the southern end of each 100 m transect (except for 5A, where they show the western end).

5.2.2 *Vegetation sampling*

Plant composition (aerial cover) was recorded annually from 2007 to 2015 in autumn by recording the plant species at each metre along two or three pairs (for paddocks 6A and 6B) of 100 m transects approximately 15 m apart. If no plant was encountered, 'bare ground' was recorded. The start of each transect was demarcated by permanent metal poles, and the transects extended 100 m (measured using a tape measure) in a northerly direction (easterly for paddock 5A). Because the ends of the transects were not demarcated, the actual position of each transect varied slightly over time.

5.2.3 *Statistical analysis*

Rainfall data are collected at the site. Monthly rainfall during the study period was illustrated related to average monthly rainfall over the long term (since 1888). A paired t-test was used to test whether the seasonal rainfall during the study period was higher than the average seasonal rainfall.

Data were relativized to 100% and Bare Ground treated as a pseudo-species. Species were classified according to longevity and growth form (Table 5.2). Species composition was described using Non-Metric Multidimensional Scaling (NMMS) using the CANOCO 4.5 package in conjunction with the WinKyst package (Ter Braak and Šmilauer, 2002) .

Directional trends in abundance of dominant growth forms and of species were determined using linear regression.

5.3 Results

5.3.1 Rainfall

Rainfall over the period followed the typical seasonal pattern where most rain fell during the summer. Seasonal rainfall from 2007-2015 was on average 508 mm per annum, significantly higher than the long-term average of 372 mm (t_9=3.59; P=0.007), and all seasons were higher than average other than 2006 (368 mm) that was very close to average. From 2007-2011 rainfall was much higher than the average (587 mm), and from 2013-2015 was above average (417 mm) (Figure 5.2). Rainfall for the previous 10 seasons had averaged 395 mm, which was not significantly different from the long-term average (t_{10}=0.693; P=0.506).

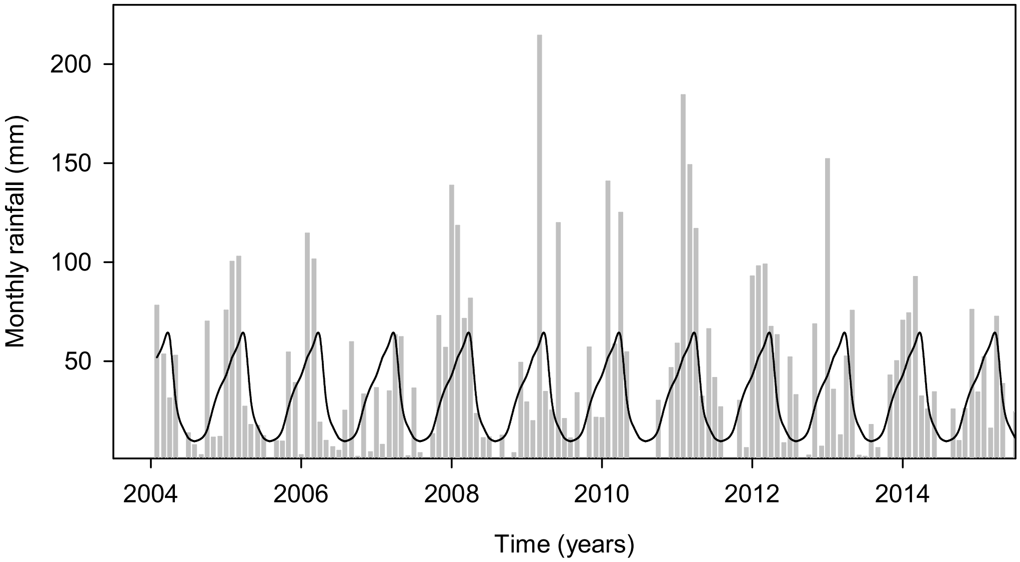


Figure 5.2. Actual (bars) and average (line) monthly rainfall at Grootfontein from 2004 to 2015.

5.3.2 Multivariate analysis of species composition

The ordination indicated that variation in species composition is smaller over time (Figure 5.3) than over space (Figure 5.4). However, there are signs that the total dissimilarity increased over time (the area of the envelopes increases in size over time in Figure 5.3). The primary axis of the ordination is a spatial one along a north-south gradient, with the composition of the hill paddocks being clearly different from the plains paddocks (Figure 5.4). The primary axis for the ordination of species composition on the plains paddocks also followed a north-south gradient. Paddocks 4A and 4B were compositionally slightly different from the other plains paddocks (Figure 5.5), which is consistent with their description (du Toit, 2002a) as "semi plain/mountain". The hills paddocks were compositionally distinct from each other (Figure 5.6) and the primary axis in the ordination follows an aspect gradient. For both the plains and the hills paddocks there was a directional shift in the ordinations away from Bare Ground (i.e. toward increased cover)

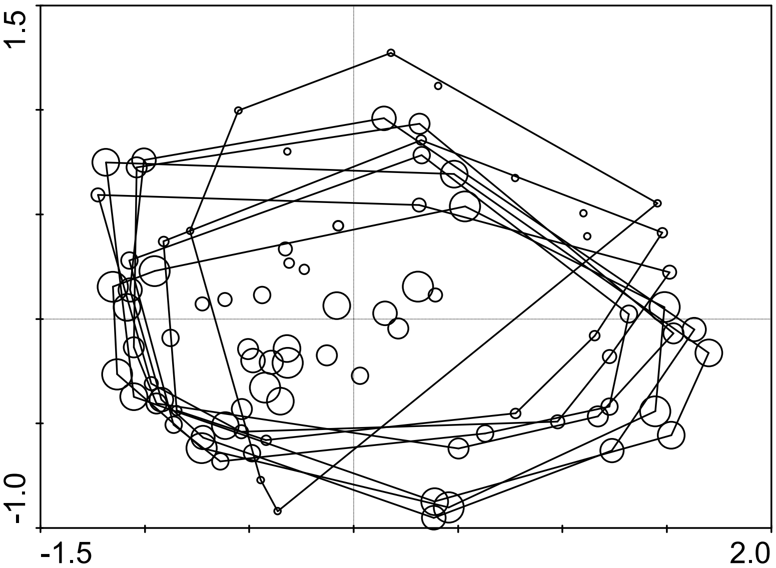


Figure 5.3. Non-metric multidimensional scaling ordination of species composition in all paddocks in all years grouped according to year (Boesmanskop, Grootfontein). Markers are scaled from smallest (2007) to largest (2015). Stress = 0.180.

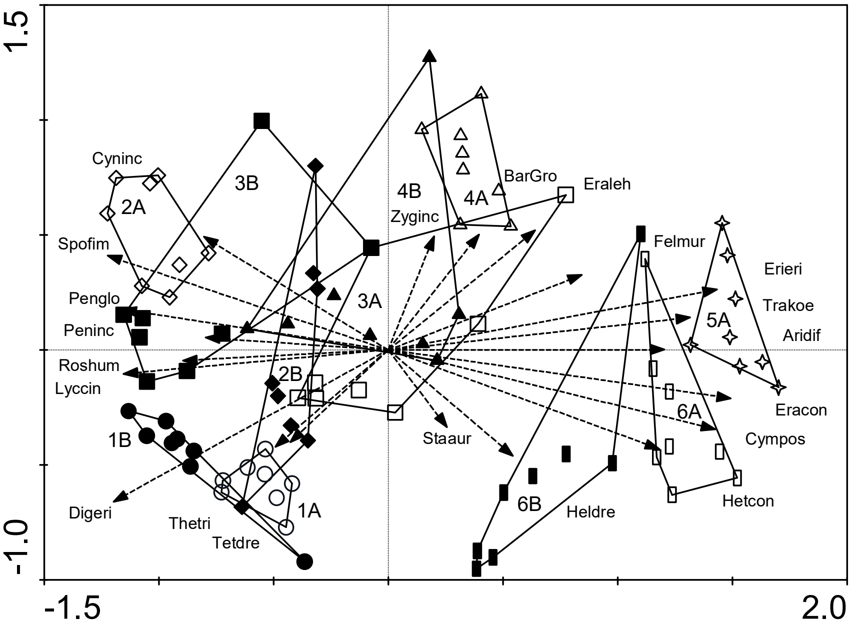


Figure 5.4. Non-metric multidimensional scaling ordination of species composition of all paddocks at Boesmanskop from 2007 to 2015. Codes are the first three letters of the genus and the species (see Appendix 1); Bargro = bare ground. Stress = 0.180.

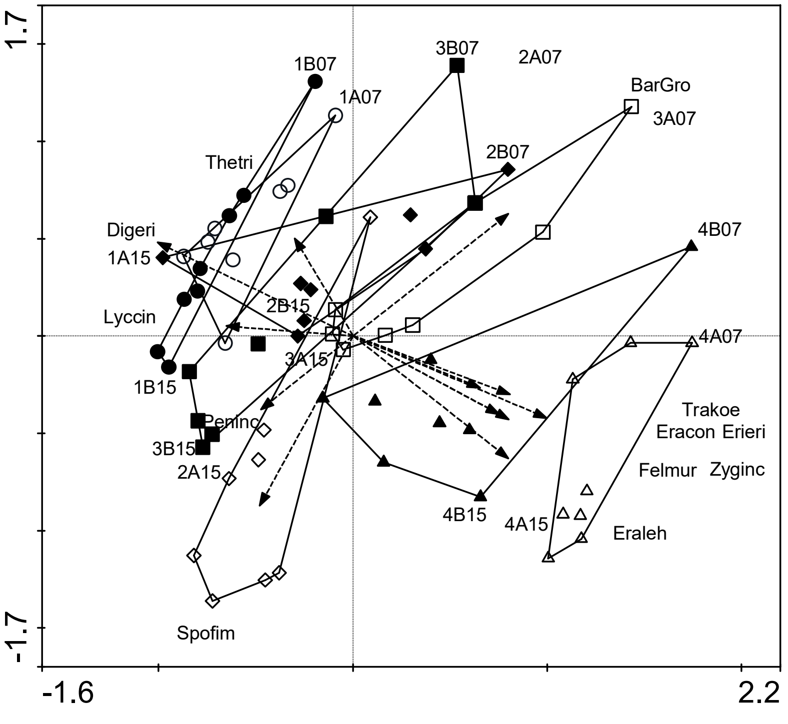


Figure 5.5. Non-metric multidimensional scaling ordination of species composition of plains paddocks at Boesmanskop from 2007 to 2015. Codes are the first three letters of the genus and the species (see Appendix 1); Bargro = bare ground. Stress = 0.203.

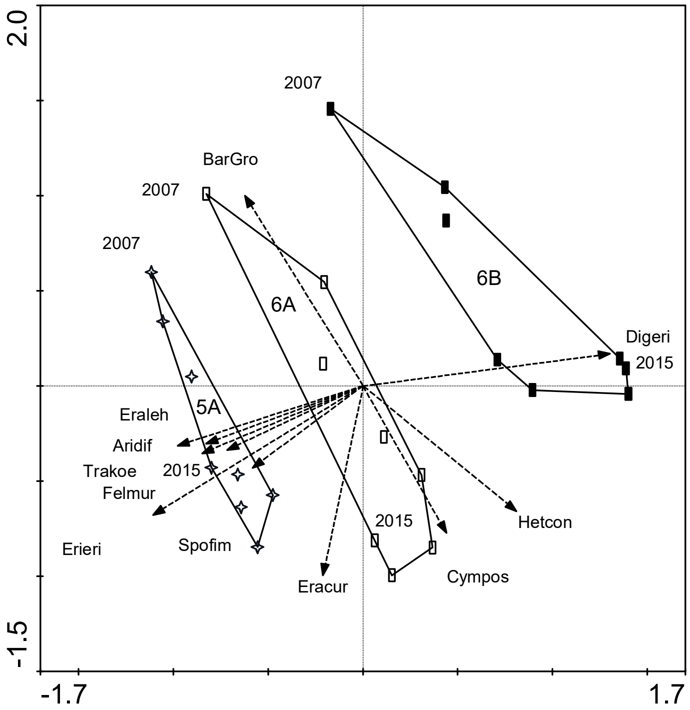


Figure 5.6. Non-metric multidimensional scaling ordination of species composition of hill paddocks at Boesmanskop from 2007 to 2015. Codes are the first three letters of the genus and the species (see Appendix 1); Bargro = bare ground. Stress = 0.176.

5.3.3 Growth forms

Grasses were the most dominant growth form on both the plains and the hills (Figure 5.7), followed by dwarf shrubs. On the hills, grass cover increased over time ($F_{1,6}$=36.1; P=0.001), while shrub cover remained approximately constant (Figure 5.8). On the plains, dwarf shrub cover increased over time ($F_{1,6}$=36.3; P=0.001), while grass cover showed a curvilinear response, increasing until 2011/12 then decreasing ($F_{2,5}$=32.2; P=0.001). Bare ground declined to approximately 0% by 2011 (Figure 5.9). Short-lived grasses had a very low incidence, and did not show any significant trends over time.

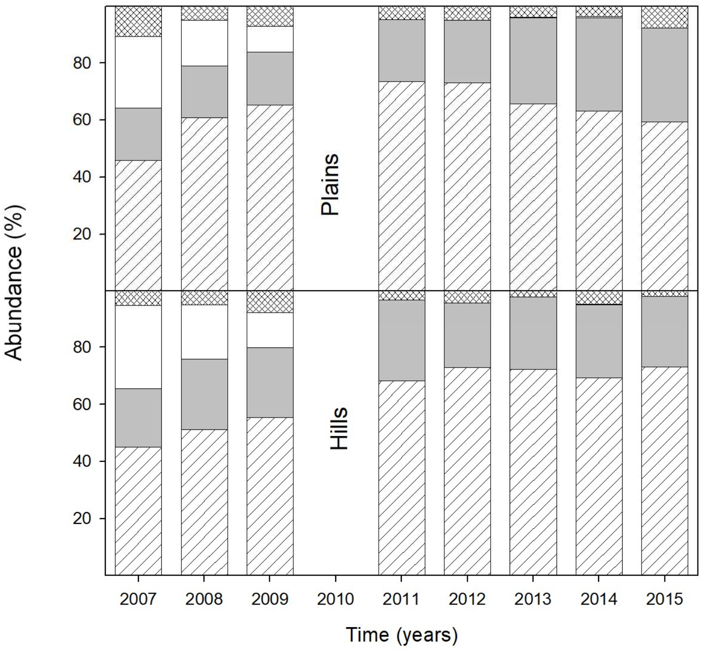


Figure 5.7 Stacked area bar graph showing the relative abundance of grass (diagonal stripes), dwarf shrubs (grey), bare ground (white) and other (cross-hash) growth forms for plains and hills at Boesmanskop, Grootfontein.

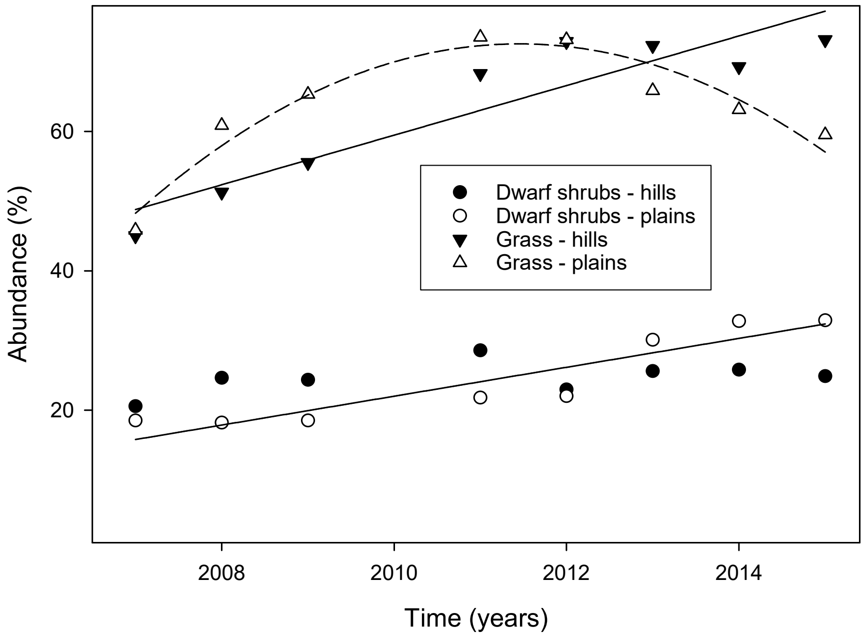


Figure 5.8. Aerial cover of the two dominant growth forms (perennials; dwarf shrubs and grasses) for hills and plains at Boesmanskop. Lines highlight statistically significant linear (solid) and quadratic (dashed) regressions.

5.3.4 Species

The five most abundant species in each paddock accounted for between 46 and 78% of all plants (Table 5.1). The perennial grass *Digitaria eriantha* was one of the top five most common species in all paddocks, and was usually the most abundant species. The large perennial grass *Cymbopogon pospischilii* was common on the hills paddocks and absent on the plains. The perennial dwarf shrubs *Pentzia globosa* and *Pentzia incana* were common in some of the plains paddocks.

On the hills 92 species were encountered of which 51 were dwarf shrubs and 18 were perennial grasses. The grasses *Eragrostis curvula* subsp *conferta* and *D. eriantha* were co-dominant (each 16%) followed by the shrub *Eriocephalus ericoides* (10%) and *C. pospischilii* (8.2%). The grasses *D. eriantha* and *Heteropogon contortus* and the shrub *E. ericoides* increased significantly over time. On the plains 91 species were encountered of which 44 were dwarf shrubs, 17 were perennial grasses, and 5 were annual herbs. The grasses *D. eriantha* (27%), *Sporobolus fimbriatus* (13%) and *Themeda triandra* (7.6%) were most common, followed by the shrub *P. globosa* (6.6%).

Table 5.1 Five most abundant species in each paddock at Boesmanskop (data from 2007 to 2015 pooled). Codes are the first three letters of the genus and the species (see Table 5.2)

SppCode	1A	1B	2A	2B	3A	3B	4A	4B	5A	6A	6B
Cympos									7.7	9.1	7.9
Cyninc			11.5					6.7			
Digeri	40.3	32.7	23.0	36.6	26.4	27.9	7.7	25.2	7.2	11.7	28.9
Eracon	3.7				6.3			7.6	20.4	11.2	16.5
Eraleh							9.5				
Erieri				5.8	5.7		10.1	8.9	14.5	12.3	
Felmur									6.6		
Hetcon										5.2	5.0
Lyccin	3.2										
Penglo		8.2	7.8	7.8		14.0					
Peninc		6.4	7.1	3.7		5.3					
Spofim	9.3	12.1	29.0	6.5	8.0	13.8	11.9	12.2			
Thetri	17.9	18.7			8.0	4.8	7.3				3.3
Total	74.4	78.1	78.4	60.4	54.4	65.7	46.5	60.5	56.3	49.5	61.6

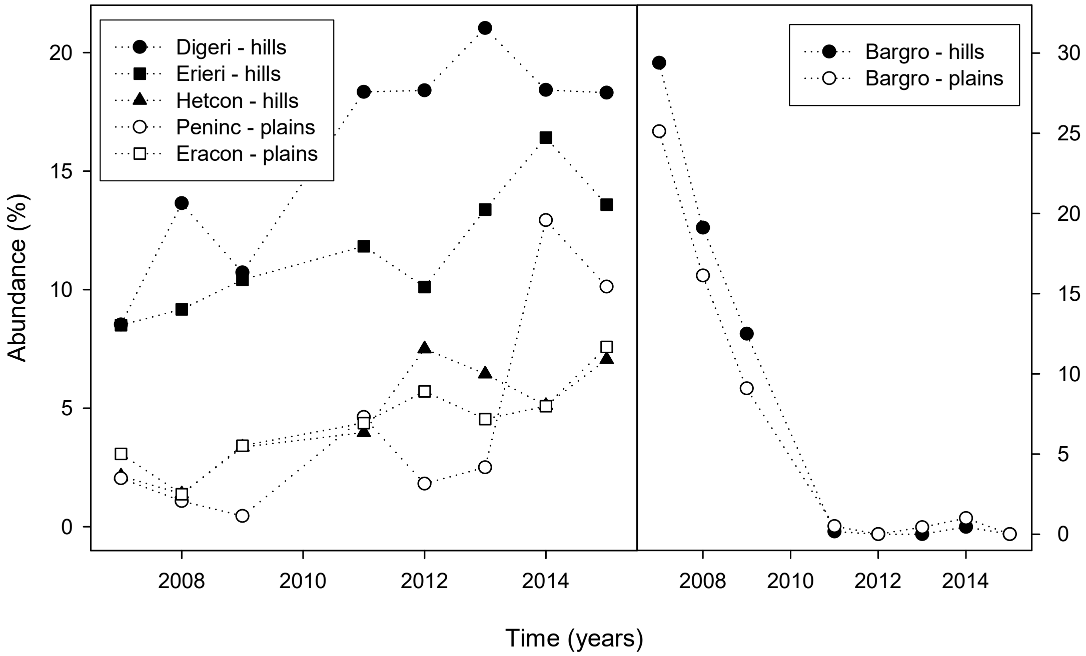


Figure 5.9. Species (and bare ground) that changed significantly in abundance over time at Boesmanskop (all $F_{1,7}>16$; $P<0.007$ except for Peninc: $F_{1,7}=7.4$; $P=0.03$). Codes are the first three letters of the genus and the species (Table 5.2); Bargro = bare ground.

Table 5.2 Species at Boesmanskop. “Abun” = average abundance over all sites over all years; ‘-‘, ‘---‘, ‘+’ and ‘+++’ indicate small or large decreases or increases over time, respectively, whether or not these are statistically significant

Life form and species	**Abun**	**Slope**
Annual cyperoid herb		
Bulbostylis humilis	0.12	-
Annual herb		
Chenopodium glaucum	0.05	
Conyza bonariensis	0.13	
Conyza canadensis	0.00	
Hermannia coccocarpa	0.03	
Salsola kali	0.02	
Annual or biennial grass		
Aristida congesta	0.28	+
Chloris virgata	0.08	
Perennial cyperoid herb		
Cyperus capensis	1.12	---
Perennial dwarf shrub		
Amphiglossa triflora	0.03	
Berkheya angustifolia	0.00	
Blepharis capensis	0.01	
Blepharis mitrata	0.01	
Chrysocoma ciliata	0.02	
Dimorphotheca cuneata	0.06	
Eriocephalus ericoides	5.78	+
Eriocephalus spinescens	0.77	+
Eriocephalus spp	0.02	
Felicia fascicularis	0.04	+
Felicia filifolia	0.11	+
Felicia muricata	2.00	+
Galenia procumbens	0.37	-
Gnidia polycephala	0.00	
Helichrysum dregeanum	0.60	-
Helichrysum lucilioides	0.01	
Helichrysum pentzioides	0.01	
Helichrysum rutilans	0.01	
Helichrysum zeyheri	0.29	+
Hermannia cuneifolia	0.02	
Hermannia desertorum	0.03	
Hermannia filifolia	0.03	
Hermannia linearifolia	0.01	
Hermannia multiflora	0.01	
Hermannia pulchella	0.01	
Indigofera denudata	0.01	
Indigofera nigromontana	0.05	
Jamesbrittenia atropurpurea	0.01	
Jamesbrittenia filicaulis	0.05	-
Justicia cuneata	0.00	
Limeum aethiopicum	0.02	-
Melolobium candicans	0.11	
Melolobium microphyllum	0.06	
Nenax cinerea	0.06	-
Nenax microphylla	0.18	+
Osteospermum armatum	0.11	

Life form and species	**Abun**	**Slope**
Osteospermum leptolobum	0.06	-
Pegolettia retrofracta	0.02	+
Pelargonium ramosissimum	0.01	
Pentzia globosa	4.90	+
Pentzia incana	2.83	+++
Pentzia pinnatisecta	0.13	+
Pentzia punctata	0.01	
Pentzia sphaerocephala	0.14	-
Pentzia spinescens	0.00	
Phymaspermum parvifolium	0.60	+
Plinthus karooicus	0.03	
Pteronia glauca	0.44	+
Pteronia sordida	0.27	-
Pteronia tricephala	0.15	+
Rosenia humilis	0.71	+
Salsola calluna	0.45	+
Selago geniculata	0.58	+
Selago saxatilis	0.50	+
Stachys aurea	0.63	-
Stachys rugosa	0.13	
Tripteris sinuata	0.19	
Wahlenbergia albens	0.13	+
Wahlenbergia tenella	0.03	-
Zygophyllum incrustatum	0.59	+
Zygophyllum microphyllum	0.01	
Perennial parasitic dwarf shrub		
Thesium hystrix	0.05	-
Perennial fern		
Cheilanthes eckloniana	0.04	-
Perennial grass		
Aristida diffusa	2.02	-
Cymbopogon pospischilii	2.38	+
Cynodon dactylon	0.11	
Cynodon incompletus	2.95	---
Digitaria eriantha	24.32	+++
Enneapogon scoparius	0.08	-
Eragrostis bicolor	0.20	+
Eragrostis curvula subsp *conferta*	6.85	+++
Eragrostis curvula	1.45	+
Eragrostis lehmanniana	2.43	+
Eragrostis obtusa	0.29	-
Eustachys paspaloides	0.14	+
Heteropogon contortus	1.28	+
Hyparrhenia hirta	0.11	+
Melica decumbens	0.01	
Oropetium capense	0.04	
Sporobolus fimbriatus	9.72	+++
Tetrachne dregei	0.94	+
Themeda triandra	6.32	---
Tragus koelerioides	1.78	+
Perennial herb		
Aptosimum procumbens	0.01	
Dimorphotheca zeyheri	0.05	
Gazania jurineifolia	0.01	

Life form and species	**Abun**	**Slope**
Hermannia pulverata	0.04	
Indigofera alternans	0.05	
Salvia stenophylla	0.07	
Perennial geophytic herb		
Moraea pallida	0.01	
Moraea polystachya	0.02	
Oxalis depressa	0.01	
Perennial shrub		
Asparagus africanus	0.05	+
Asparagus suaveolens	0.01	
Lycium cinereum	1.60	+
Perennial succulent		
Mestoklema tuberosum	0.07	-
Ruschia grisea	0.06	
Trichodiadema pomeridianum	0.19	-
Perennial succulent dwarf shrub		
Hertia pallens	0.01	
Kleinia longiflora	0.03	
Ruschia intricata	0.50	-
Sarcocaulon salmoniflorum	0.05	+
Perennial succulent herb		
Senecio radicans	0.01	
Tripteris aghillana	0.55	+
Perennial tree or large shrub		
Diospyros austro-africana	0.00	
Searsia erosa	0.01	

5.4 Discussion and conclusions

Considering all data from all years, the botanical composition at Boesmanskop remained relatively constant over time. There was notable spatial variation, particularly between hill sites and plains sites, and to a lesser extent between sites adjacent to the hill sites and those not, reflecting the high natural diversity of Nama-Karoo vegetation (Mucina, Rutherford, *et al.*, 2006). Compositional changes over time at individual sites showed a shift towards increased cover which reflects increased rainfall.

Total cover on both the hills and the plains matched each other almost exactly, with nearly total cover being achieved, and maintained, after four years of high rainfall. This is unusual in Karroid vegetation, where bare ground is usually a prominent feature (Cowling and Roux, 1987; Milton and Hoffman, 1994; Keay-Bright and Boardman, 2006). This increase in cover may have important implications for the potential incidence of fire in the Karoo. First, the increase in cover presumably equates with an increase in biomass which would influence the potential intensity of fires. Second, and likely more importantly, the increase in cover represents an increase in the continuity of a fuel load. Continuity of fuel is a major determinant of the ability of a fire to spread (Cheney and Sullivan, 2008). Thus the well-documented relation between fire and rainfall in Karoo environments (Edwards, 1984; Cowling and Roux, 1987) relates not only to the amount of grass that is produced, but likely also to the structural characteristics of that fuel load.

On hill sites, cover of the dwarf shrub component remained approximately constant while the cover of grasses, notably the large, palatable tufted species *Digitaria eriantha* and *Heteropogon contortus*, increased. At a species level, the common shrub *Eriocephalus ericoides* increased, reflecting the ability of this species for rapid growth (Hobson and Sykes, 1980), typical of species that cannot resprout (Midgley, 1996). There was no indication of a decline in plant cover in the hills once the very high rainfall period (2007-11) ended and more typical rainfall patterns resumed. The mechanism underlying the hardiness of rocky, steep veld has not been explored, though their ability to resist drought has been documented (Anon, 1983).

On the plains, veld shrub and grass cover increased with increasing rainfall until 2012, after which grass cover declined and shrub cover continued to increase slightly. Much of the shrub increase was due to increases in cover of *Pentzia incana*. This species is associated with the Karroid invasion of grassland areas (Acocks, 1953), owing in part to its ability to rapidly vegetatively propagate by rooting where stems touch the ground (termed ‘layering’), hence the common name Ankerkaroo (“Anchor Karoo”). The concomitant increase in shrubs and grasses when entering a time a higher than normal moisture availability is in contrast with a general notion that grasses necessarily out-compete dwarf-shrubs, at least in the short-term. Monitoring of Karroid veld for longer periods of time under conditions of prolonged high moisture availability would be needed to understand this process. The decline in grasses at the expense of shrubs may be a function of the latter’s ability to better tolerate drought conditions.

Regarding the hypotheses posed:

1. Total vegetation cover did increase with increasing rainfall;
2. The incidence of short-lived species was too low to determine any trends in cover;
3. The cover of perennial grasses increased with increasing rainfall; and
4. The cover of shrubs as a growth form increased on the plains but not on the hills.

CHAPTER 6 MINIMUM TEMPERATURES AND FROST AT GROOTFONTEIN IN THE EASTERN KAROO, SOUTH AFRICA, OVER 98 YEARS

6.1 Introduction

Minimum temperature is an important determinant of vegetation organisation and ecological processes in natural and agricultural environments. Local minimum temperature conditions determine, in part, the distributions of the world's biomes because of the cold tolerance, chilling requirements and heat requirements of plants, and its interaction with water availability (Prentice *et al.*, 1992; Andrews, 1996; Woodward *et al.*, 2004). Global climate change is set to modify existing minimum temperature regimes, generally manifested as an increase in minimum temperatures (i.e. general warming) (Easterling *et al.*, 1997; Abatzoglou and Kolden, 2011). However, other global cyclical phenomena, such as the El Niño Southern Oscillation, also influence patterns of minimum temperatures (Gelcer *et al.*, 2013). Analyses of temperature data since approximately 1960, spanning 40–50 years, have revealed that minimum temperature changes consistent with general warming were evident across much of southern and west Africa (Kruger and Shongwe, 2004; New *et al.*, 2006; MacKellar *et al.*, 2014; van Wilgen *et al.*, 2015). The predicted effects of increasing temperatures in South Africa have been well documented, and the predicted effects of increasing minimum temperatures *per se* have received some attention in terms of their likely effects on botanical composition (Rutherford *et al.*, 1999).

Some plant species are injured by chilling (cold but above-freezing conditions) (Kratsch and Wise, 2000), some species die in a light frost, when temperatures are at or near 0°C, whereas others are far more freezing tolerant, surviving temperatures of less than -40°C. Some plant fragments can survive cryogenic freezing in liquid helium at -270°C, a temperature far lower than occurs naturally on Earth (Sakai, 1965). In South Africa, species from the Nama-Karoo Biome are generally much more cold-hardy than are Albany Thicket species, a functional trait that may delineate the boundary between the two biomes (Duker, Cowling, du Preez, and Potts, 2015; Duker, Cowling, du Preez, Vyver, *et al.*, 2015). This finding follows that of Rutherford (2006), who suggested a similar effect may occur at the interface between the Nama-Karoo and Desert Biomes. Although generally cold-hardy, Donaldson (1989) found that seedlings of many Karroid species (both shrubs and grasses) were damaged or killed at temperatures of -

6.7 and (more so) at -7.9°C, highlighting the important effects that minimum temperatures may play in the population dynamics of species inhabiting cold areas.

In agricultural production systems in the Karoo, frost can have important direct or indirect effects on livestock. Livestock, notably Angora goats, may die during cold spells (Snyman and van Heerden, 2011), and spatially descriptive models have been developed to qualify such risks in the Eastern Cape (Rowswell, 1985). Low temperatures can indirectly affect animal health and food availability. Several pathogens are influenced by low temperatures: severe frosts temporarily eliminate insects (mosquitos and midges) that carry the Rift Valley Fever, Wesselsbron and Blue Tongue viruses (Joubert, 1988), while the incidence of coccidiosis can be greatly reduced under frosty conditions (Wentzel, 1989). High or low temperatures may affect the timing of the hatching of insect eggs, which may influence the occurrence of locust outbreaks, an episodic event in the Karoo (Henschel, 2015), and hence affect forage availability. In some semi-arid grasslands, the onset of frost can mark a sharp decline in grass forage quality (Snyman, 2004), and low temperatures can damage drought fodder crops such as spineless cactus (Bosman, 1942). Early frosts coupled with late rains can result in very short growing seasons (Mucina, Rutherford, *et al.*, 2006), and hence reduced grass availability (most Karoo shrubs are C_3 species, and are not affected by frost to nearly the same extent). Unseasonal frosts can have unexpected effects on livestock, such as the development of acidosis in sheep allowed to browse frost-damaged maize (Bath, 1975), while late frosts (i.e. frosts that occur long after the penultimate frost of the season) can kill established frost-sensitive crops such as tomatoes and cucurbits, which are common in the Karoo.

The objectives of this paper are twofold. First, it aims to examine long-term patterns of minimum temperatures for Grootfontein in order to identify the potential importance of this variable for livestock production and for ecological change. Second, it aims to examine temporal trends in minimum temperature within the context of datasets of adequate length for climate change predictions for the country. A single-site study of this nature, in contrast with more common regional descriptions, is useful because a) the dataset is long (from 1916), allowing long-term trends to be scrutinised, b) it provides a useful platform for interpreting agricultural and ecological events that have been recorded in detail on long-term trials (since the 1930s) at the site, and c) it explores a parameter (minimum temperature) that, despite being ecologically and agriculturally important, has received much less attention than other variables such as rainfall.

6.2 Methods

This study took place at the Grootfontein Agricultural Development Institute, 2.3 km north-east of Middelburg (31.47826°S; 25.02001°E; 1264 m.a.s.l.). The site is in the Eastern Upper Karoo (Mucina, Rutherford, *et al.*, 2006), and is situated in the ecotone between the Nama-Karoo Biome to the west and Grassland Biome to the east. Minimum temperature data were obtained from the South African Meteorological Office and the Agricultural Research Council for the period 1916–2014. Data from any particular year were included into the dataset if there were records for at least 360 days or, in the case of 2002 and 2003, at least 326 days because only summer data were missing. This meant that the years 1918, 1935, 1946, 1999–2001, and 2014 were excluded to yield a 92-year data set. A day was defined as having had frost if the minimum temperature, measured in a Stevenson screen at approximately 1.25 m above ground, was below zero degrees. Unless stated, 'temperature' refers to minimum temperature. Seasons are defined as summer (December to March), autumn (April to May), winter (June to August) and spring (September to November), following du Toit and O'Connor (2014).

Statistics reported here include seasonal and monthly average temperatures; temporal distribution and patterning of sub-zero temperatures; number of frost nights per year and average number of frost nights per month; probability distributions of first and last frost; date of first and last frost per year, duration of the frost (dormant) season; and distribution of late frosts over time.

The probability of the timing of first and last frosts of the season of an 'average year' was calculated by calculating the probability of frost on any day of the year (Equation 6.1), from which probability of frost not occurring on that day follows (Equation 6.2). The probability of having not had frost by a certain date from 1 Jan is the product of the daily probabilities of no frost up to that date (Equation 6.3), and therefore the probability of having had frost by a certain day is that value subtracted from one (Equation 6.4). The chance of a particular date (after 1 July) having received the last frost of the season is calculated in a similar way, but by reversing the time series from 31 December to 1 July.

Time series of minimum annual temperatures, dates of first and last frosts, duration of growing season, and late frosts were filtered using the Lowess smoothing (α=0.25), a robust regression technique that protects against the effect of outlying points (Cleveland, 1979).

Lowess regressions were conducted using dedicated software (Peltier, 2016), and other statistical analyses were conducted using StatGraphics (Statpoint Technologies Inc, 2009). Figures were generated using SigmaPlot (Software Systat Inc, 2001).

$$F_d = {}^{n_f}/_{n_t}$$

Equation 6.1

$$N_d = 1 - F_d$$

Equation 6.2

$$S_{N_d} = \prod_{i=1}^{d} N_d$$

Equation 6.3

$$S_{F_d} = 1 - S_{N_d}$$

Equation 6.4

where F_d is the probability of frost on any day, n_f is the number of occurrences of frost on any day *d*, n_t is the total number of records for any day *d*, N_d is the probability of frost not occurring on any day *d*, S_{Nd} is the cumulative product of all probabilities of no frost from 1 Jan to day *d*, and S_{Fd} is the probability of having had frost by day *d*.

6.3 Results

6.3.1 Minimum temperatures

Average monthly temperatures followed a unimodal distribution over the year, highest in February and lowest in July (Table 6.1). Average temperatures were above zero for all months other than July, with variation of temperatures highest in August and lowest in January. Temperatures were lowest in winter followed by autumn and then spring, and highest in summer (Figure 6.1). The variation of summer temperatures was lower than that of the other seasons, and was more strongly peaked (higher kurtosis). The lowest-ever recorded temperature in summer was only slightly below zero (-1.1 °C), whereas it was below -8 °C for all of the other seasons (Spring -8.9, Autumn -9.4, and Winter -12.6 °C). (Shapiro-Wilk tests had revealed that all monthly and seasonal temperature data were normally distributed.)

Temperatures of at least -4 °C have occurred every year on record, and temperatures of at least -6 °C have occurred every year except for 1922, 1929, 1932, and 1998 (Figure 6.2). Temperatures between -8 and -10 °C were less common, having occurred on 151 nights since 1916. Frosts of between -10 and -12 °C have occurred 27 times, and once (in 1956) there was a temperature of below -12 °C.

The distribution of below-zero temperatures does not appear to be random, but clumped across years (Figure 6.3). Temperatures of between -2 and -4 °C occur approximately 20 times a year. Temperatures between -4 and -6 °C were strongly associated with period from 1930 to 1960, and this trend was also evident for the -6 to -8, -8 to -10 and -10 to -12 °C classes. This indicates that the 1930s, 40s and 50s were much colder than other periods in the record. For example, temperatures between -10 and -12°C occurred in nine years of the years between 1943 and 1958, with one year (1954) having six such frosts. In contrast, from 1916 to 1942 (25 years; 2 without data) and from 1959 to 2013 (55 years; 3 years without data) temperatures dropped to these levels in only four years and three years respectively (twice in 1996). Very recently (2011–2013) there has been a higher than average number of frost days, though none below -10 °C (Figure 6.3).

Table 6.1. Average minimum temperatures (°C) and standard deviations at Grootfontein

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Average	12.8	12.8	10.9	6.82	3.15	0.21	-0.42	1.23	3.96	6.76	9.21	11.4
Standard Deviation	3.19	3.32	3.61	4.13	4.27	4.38	4.54	4.92	4.90	4.44	3.82	3.37

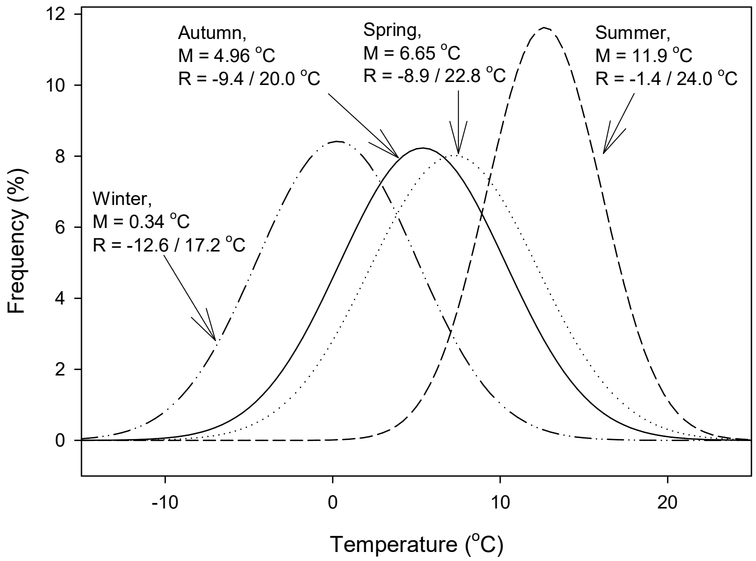


Figure 6.1. Seasonal minimum temperature distributions at Grootfontein annotated with the mean minimum temperature (M) and the range (R; min / max) (°C).

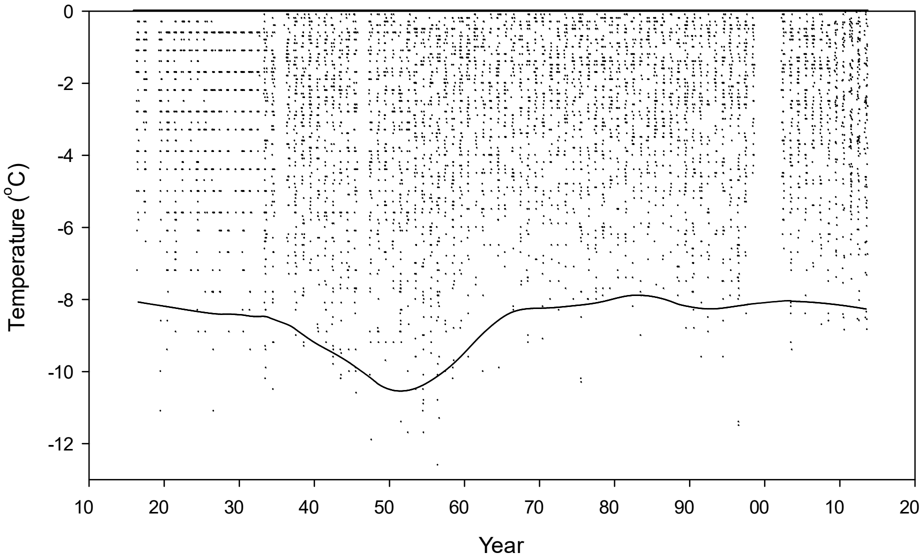


Figure 6.2. Time series (1916-2013) of all below-zero minimum temperatures (°C) at Grootfontein. Solid line is lowest annual minimum temperature smoothed using a Lowess function.

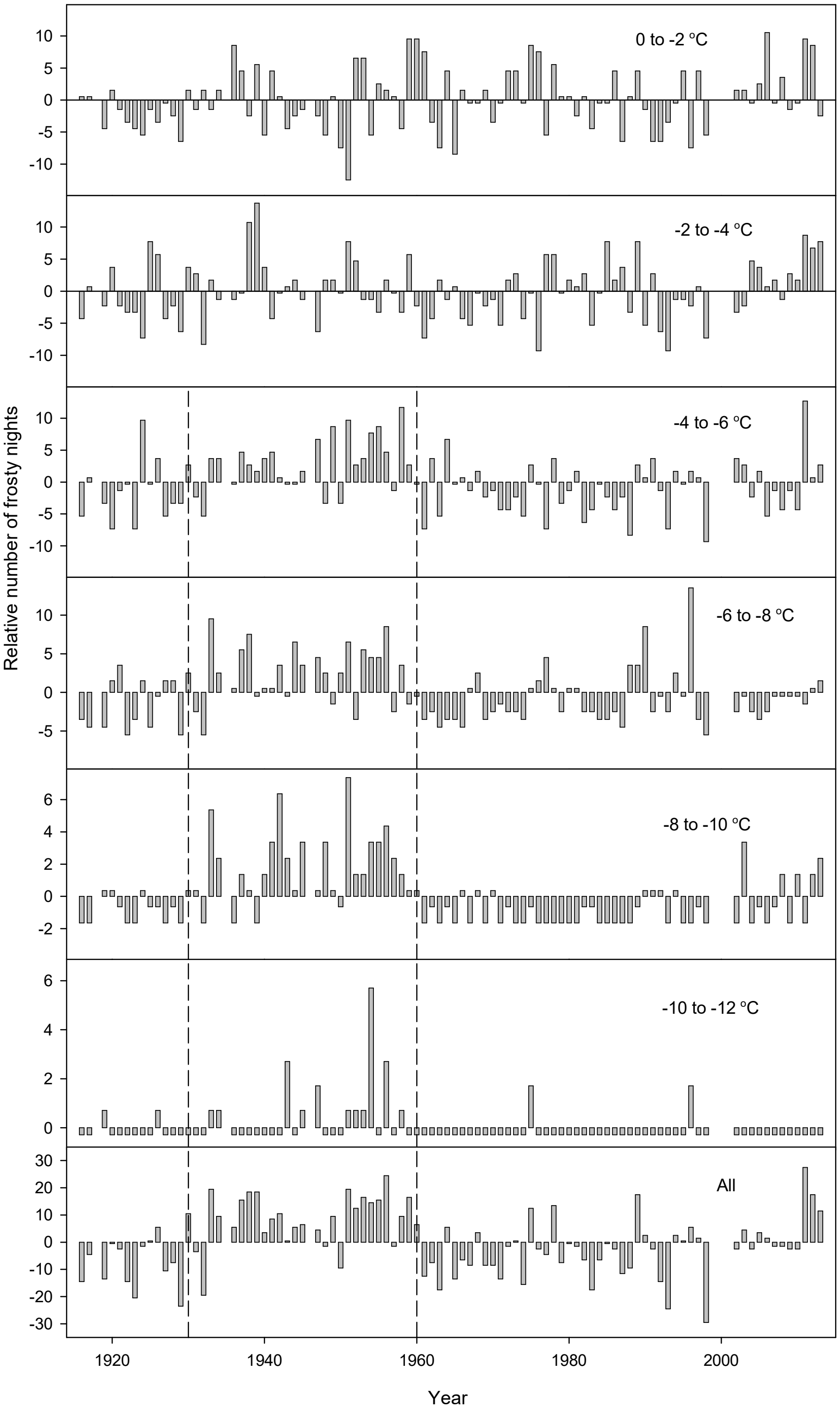


Figure 6.3. Number of frosty nights (relative to the average number of frosty nights), stratified into 2-degree temperature classes, at Grootfontein. The taller a bar, the greater the number of cold nights in that year. Vertical dashed lines demarcate the particularly cold period from 1930–1960.

6.3.2 *Frost*

In 93% of years the first day of frost was either in April or May, rarely in March or June, and once in January (Table 6.2). The winter months of June, July and August had the highest number of frost days (Figure 6.4). May and September had approximately seven days of frost each, and April and October about two days each. Frost during the other months was very unlikely. Although the average number of frost days in April was low, the probability of it occurring at least once in that month was high. The day with the highest likelihood of frost was 12 July (67% chance), and the week with historically the highest number of frosts is from 11–17 July. The likelihood of having had at least one frost by a particular date is presented in Figure 6.5 (all data pooled, temporal patterns ignored). The first week of April is the last time in the season that is likely to be frost-free, and by the third week of April there is more than a 50% chance of at least one frost having occurred, while the chance of not yet having experience a frost by the end of the first week in May is very low. In terms of frost in spring, there remains a significant risk of frost up until the third week of October. In 90% of years last frosts will have occurred by the first week of November. Accordingly, frost-sensitive crops should not be planted until the last week of October.

On average there were 62 days of frost per year, ranging from 33 in 1998 to 90 in 2011. The period from 1916–1932 had a relatively low number of frost days, followed by a period of above-average number of frost days from 1933 to 1960, and another below-average period from 1961 to 1993 (Figure 6.3).

The dormant season is defined as the period from the first frost of the year to the last frost of the year, and is the opposite of the growing season, which is the duration of the frost-free period. On average the dormant season was 166 days – about five-and-a-half months – ranging from 116 days in 1993 to 221 days in 2002 (the outlier first frost on 20 January 1936 has been omitted from these calculations).

The date of first frost, the date of last frost, and the duration of the dormant season varied over time (Figure 6.6). The dormant season from 1936–1969 was on average 179 days, and coincided in general with the higher number of frost nights during that period. The dormant season before that (1916–1934) and after that (1970–2013) was shorter, averaging 164 and 167 days, respectively. Treating years as independent samples, the length of the dormant season from 1936-1969 was significantly longer than during other years ($P=0.027$; $F_{1,90}=5.04$).

The lateness of frost is defined as the time between the penultimate and the last frost of the year. The mean time between the penultimate and last frost of the season was 11.3 days. The median value is 6.5 days, indicating that in about 50 percent of seasons the last frost occurs within a week of the penultimate frost. Approximately 90% of the time the last frost will occur within 4 weeks of the penultimate, but some very late frosts have occurred. In eight of the 92 seasons on record the period was over 32 days or more, and in 1927, 1964, and 1997 this value was over fifty days (Figure 6.7).

Table 6.2. Frequency of occurrence of months receiving the first day of frost in each year

Month	Number	Cumulative number	Percent	Cumulative percent
Jan	1	1	1.09	1.09
Feb	0	1	0.00	1.09
Mar	3	4	3.26	4.35
Apr	55	59	59.78	64.13
May	31	90	33.70	97.83
Jun	2	92	2.17	100.00
Jul	0	92	0.00	100.00

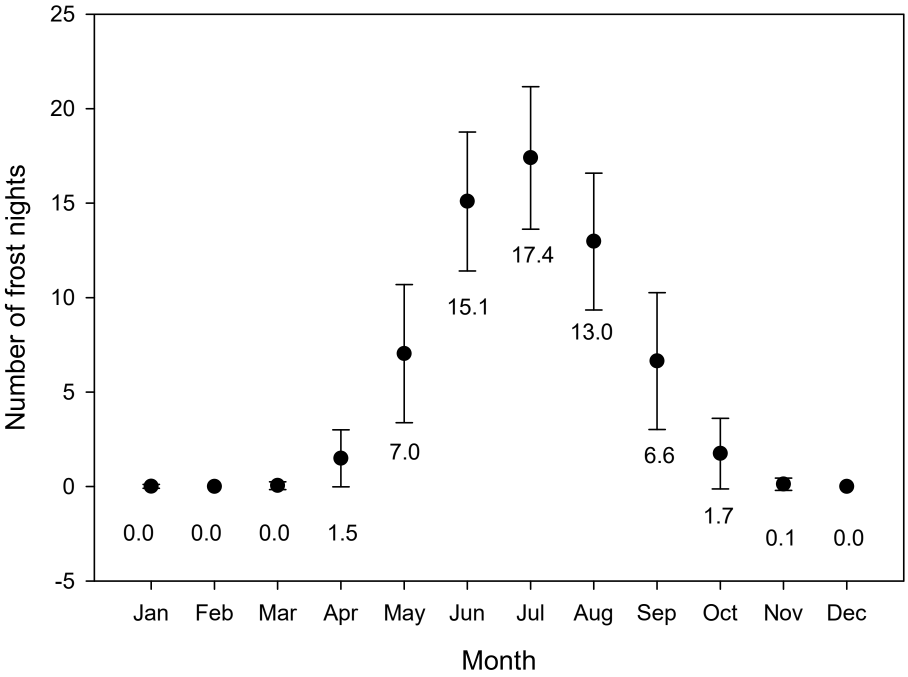


Figure 6.4. Average number of frost days per month at Grootfontein. Error bars are +/- 1 SD.

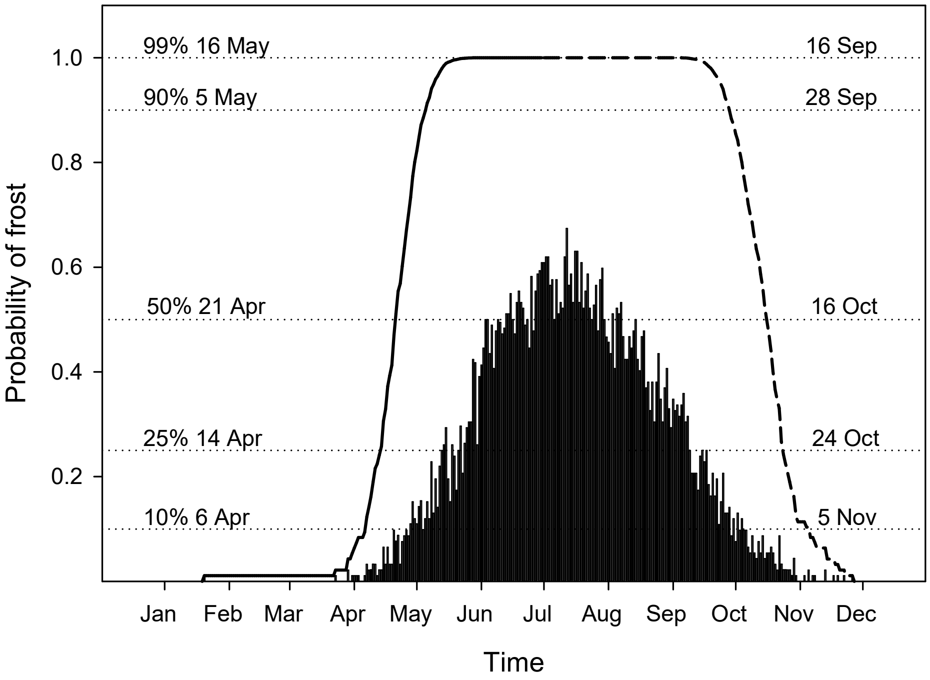


Figure 6.5. Daily probability of frost (columns), cumulative probability of frost after 1 January (solid line; left hand column of dates) and probability of a day not being the last day of frost after 1 July (dashed line; right hand column of dates) for an ‘average year’ at Grootfontein.

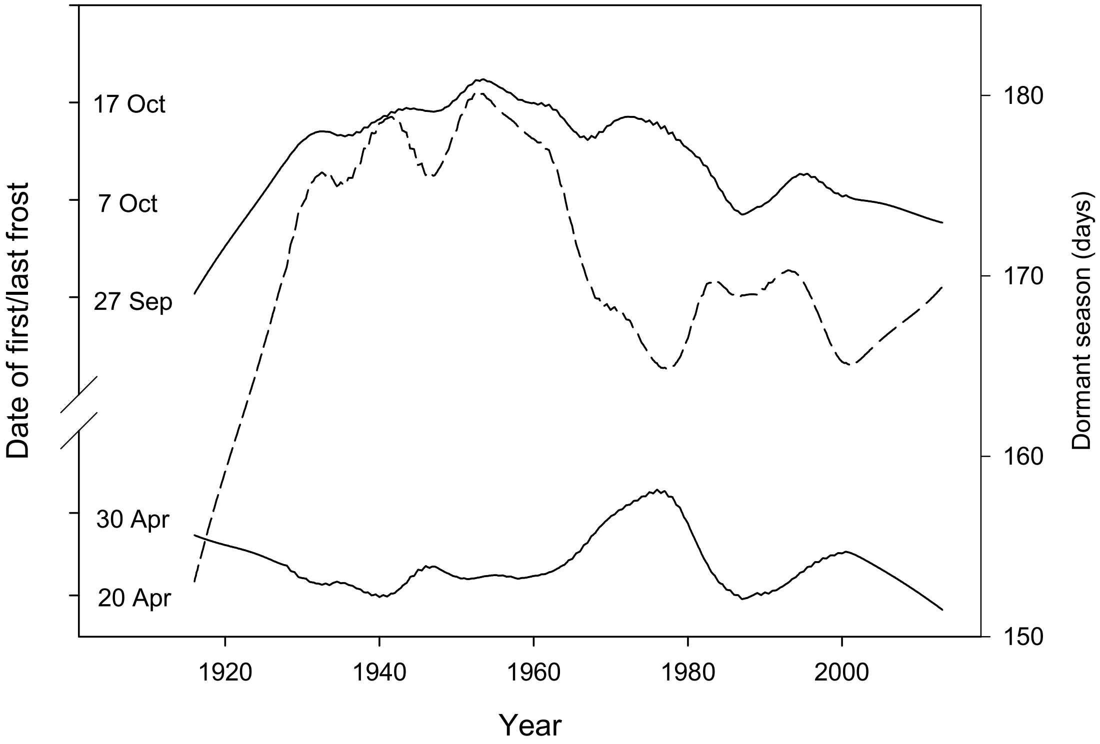


Figure 6.6. Beginning and end of dormant season (solid lines), and length of dormant season (dashed line) described using Lowess smoothing at Grootfontein.

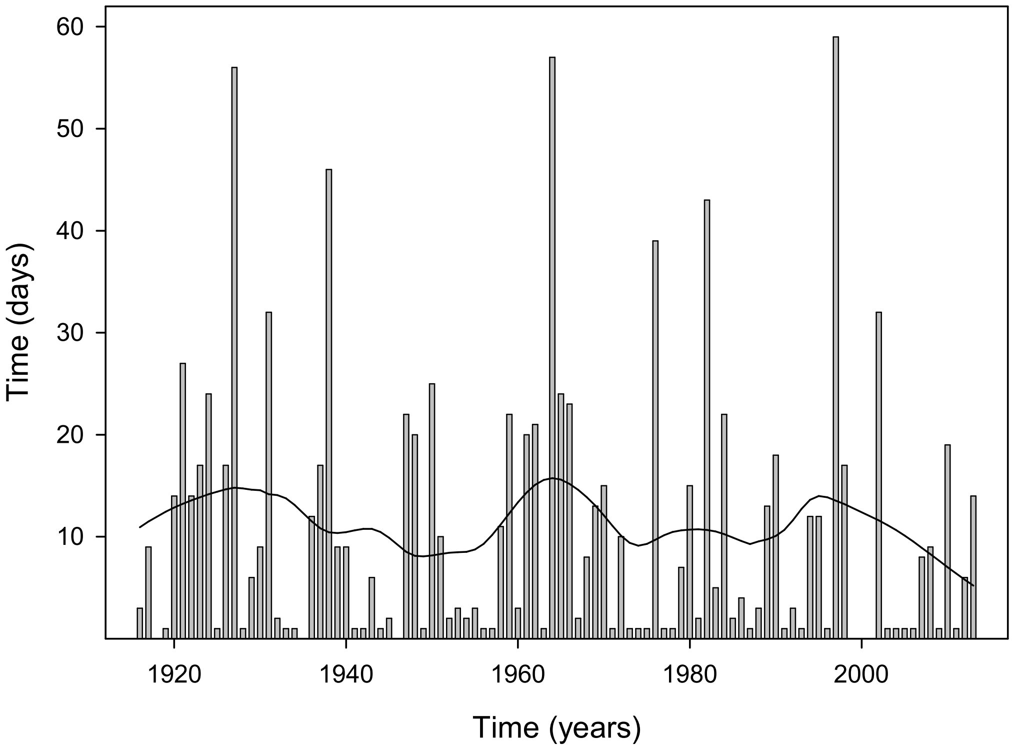


Figure 6.7. Time between penultimate and last day of frost at Grootfontein; tall bars indicate very late frosts. Solid line show data smoothed using a Lowess function.

6.3.3 Length of dataset

This dataset spans nearly a century (1916–2014). Over this time, there was no significant linear (y=a+bx) or unidirectional trend in either the number of frost days ($F_{1,90}$<0.005; P=0.96) or the annual minimum temperatures ($F_{1,90}$=3.4; P=0.069) (Figure 6.8). In contrast, there was a highly significant cubic ($y=a+bx+cx^2+dx^3$) response for both the number of frost days ($F_{3,88}$=9.77; P<0.0001) and minimum temperatures ($F_{3,88}$=6.84; P=0.0006). (In both cases, Akaike's Information Criterion shows that the cubic regression is better (P<0.01) than the linear despite the higher number of terms.) In contrast, 40-year (1951–1990) subsets of the data showed highly significant linear regressions for number of frost days ($F_{1,38}$=7.57; P=0.009) and for minimum annual temperatures ($F_{1,38}$=25.13; P<0.0001), which would be consistent with trends in global warming.

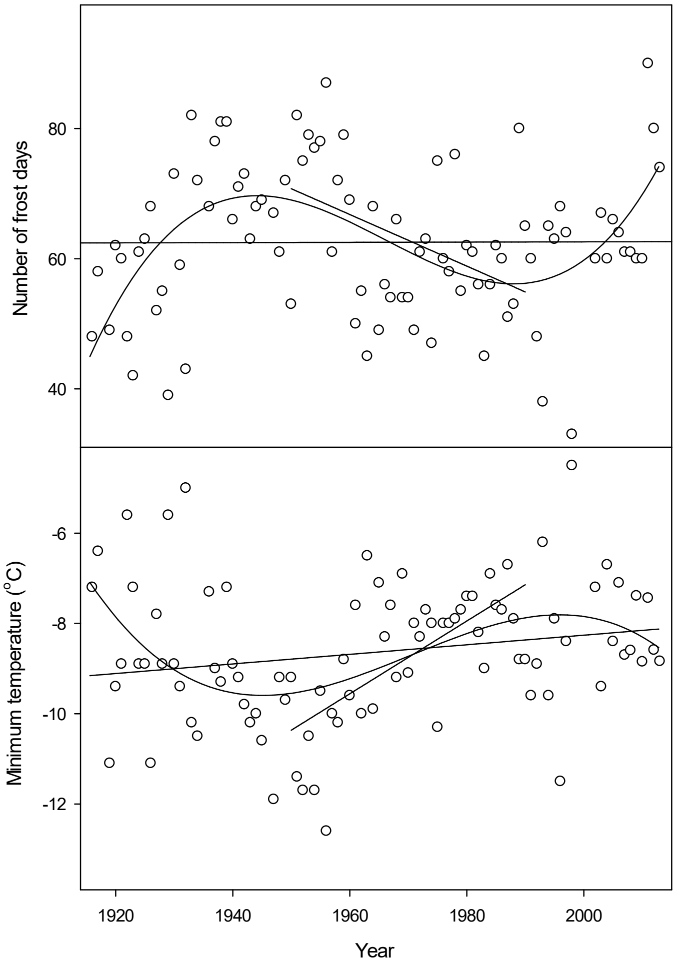


Figure 6.8. Time series of number of frost days (top) and minimum annual temperature (°C) (bottom). Lines are regressions: linear (long straight line), cubic (curved line) and data from 1951–1990 (short straight line).

6.4 Discussion

Minimum and frost data from Grootfontein support the general notion of the eastern Karoo experiencing warm summers and cold and frosty autumn, winter, and spring seasons, although just how cold it gets may be underestimated. For example, the Grootfontein annual average of 62 frost nights per year and the common occurrence of nights well below -5°C suggest colder conditions than those given as the norm (52 days and -5°C minimum) for the Nama-Karoo Biome (Mucina, Rutherford, *et al.*, 2006).

While it is well known that cold temperatures can affect natural vegetation, crops and livestock, there is little published literature on this originating from South Africa. For livestock, it is expected that effects of cold conditions would be most pronounced in Angora goats, which have a congenital condition that inhibits their ability to keep warm (Cronje, 1992), and are prone to die particularly after shearing (Hetem *et al.*, 2009). During the 1990s, it was estimated that about 6000 Angoras died per year from cold (Snyman and van Heerden, 2011), but reliable statistics are lacking, despite common reports on livestock mortality from cold (e.g. Erasmus et al. 2012). In colder countries such as Belgium (Van Laer *et al.*, 2015), France (Morignat *et al.*, 2015), Italy (Caroprese, 2008), and Mongolia (Rao *et al.*, 2015) the importance of cold, and protection from cold, on livestock are well recognised. In South Africa, perhaps, cold-induced mortality of livestock is not considered particularly important, perhaps because (other than in Angoras) losses are relatively small, losses can be mitigated with appropriate management, or cold conditions are infrequent. If there is an increase in cold weather spells in South Africa resulting from the anticipated increase in extreme temperatures linked to global warming (Alexander *et al.*, 2006), then the issue of cold weather and livestock may receive more attention.

The likely impacts of patterns of low temperatures on natural vegetation can be anticipated with more confidence owing to a greater research focus on this subject. Both non-Karroid and Karroid species are differentially impacted by frost – for example Duker *et al* (2015) showed that certain species of *Crassula* and *Felicia*, that are common inhabitants of frost-prone areas and thus assumed generally cold tolerant, were more severely damaged by exposure to -10°C treatments than when exposed to -7°C. Earlier, Donaldson (1989) had presented similar findings, and there are further examples from elsewhere in the world (Sakai and Wardle, 1978; Read and Hill, 1989; Sklenář *et al.*, 2012). It follows, therefore, that the single lowest temperature experienced in a season is important in terms of potential dieback of vulnerable species, such as was found by Muller *et al.* (2016) and the size of this effect should be magnified if such temperatures are experienced for several years running. The cold period from the 1930s to 1950s at Grootfontein should therefore have provided harsher survival conditions for sensitive plants than the comparatively benign period thereafter. Whether this was in fact the case will only be revealed if compositional data from the period are scrutinised with this in mind.

There are other potential implications of the parameters examined at Grootfontein. Early frosts would mean early curing and hence flammability of grass, which may lead to fires (du Toit, O'Connor, *et al.*, 2015). Long dormant seasons may delay planting of crops (albeit this is uncommon in this area), and late frosts occasionally kill young established crops such as pumpkins, as happened following a late frost in 2015 (Rob Southey, Lucernedale Farm, Personal Communication 2016).

While there is little evidence of linear directional trends of minimum temperatures or number of frost days over the full data record at Grootfontein, there is strong evidence of directional trends over subsets of the data. This highlights that significant trends found in relatively short datasets (40–55 years) may misrepresent longer-term patterns, especially as longer-term climatic trends and cycles are well known (Nicholson, 2001; Kane, 2009). The quadratic-type response over time may, in turn, hint at some form of long-term cycle which, if present, would imply that a cold period reminiscent of the 1930s to 1950s may return, though this of course may be strongly influenced by the general warming effects of climate change.

6.5 Conclusion

Temperatures were strongly seasonal, peaking in midsummer and reaching a minimum in midwinter. The 1930s, 40s and 50s appear to have been colder than other decades. During this time there was a higher incidence of a) very low temperature and b) frost days. Because of the detrimental effect of very low temperatures on plants, changes in frost intensity over time may be important (and understudied) drivers of agricultural production and ecosystem functioning in the Karoo. The absence of directional linear trend here is not an argument against climate change, but indicates that datasets of approximately 40 years are likely insufficient for climate variables of the nature of the Grootfontein data, owing to their pattern of temporal variability.

CHAPTER 7 FIRE EFFECTS ON VEGETATION IN A GRASSY DWARF SHRUBLAND AT A SITE IN THE EASTERN KAROO

7.1 Introduction

The Nama Karoo Biome covers much of the western interior of South Africa, ranging from arid in the west to semi-arid in the east. It is characterized by a dominance of dwarf shubs and a general absence of trees, and a grassy component whose abundance is positively related to annual rainfall (Mucina, Rutherford, *et al.*, 2006) especially if the rain falls during the warm summer months (Roux and Vorster, 1983b; O'Connor and Roux, 1995). It is bounded on the north by desert and savanna, and semi-arid grasslands on the east. Major ecological disturbances include droughts (Booysen and Rowswell, 1983) and herbivory, mainly by livestock (Milton and Hoffman, 1994), and by wildlife and occasional locust swarms (Todd *et al.*, 2002).

There is a general perception that the eastern Karoo (Hoffman *et al.*, 1995) has shifted from being dominated by perennial grasses at some time in the past (estimates range from 1400 to 1880) to being increasingly shrub-dominated (i.e. largely grass-free) since the early 20th century, owing mainly to the selective grazing habits of large numbers of livestock (Hoffman *et al.*, 1990; Bond *et al.*, 1994). It has been predicted that this 'desertification' will continue into the future (du Toit *et al.* 1991). Hoffman *et al.* (1990) and Hoffman *et al.* (1995), however, provide evidence that areas in the eastern Karoo are rather increasing in grassiness, and attribute this in part to increased rainfall. At Grootfontein in the eastern Karoo (the site of this study), rainfall was significantly higher between 1990 and 2010 (du Toit, 2010), concomitant with an increase in grassiness of the region (du Toit, 2013). Additionally, with increases in atmospheric carbon dioxide concentrations, arid and semi-arid rangelands may become increasingly grassy as C_4 grasses become more water-use efficient and therefore less prone to desiccation (Morgan *et al.*, 2011). Grassiness in the eastern Karoo is important because grasses provide fuel for fires. The shrub-dominated nature, low incidence of lightning, and low rainfall in the Karoo for most of the twentieth century (Manry and Knight, 1986) meant that fire was absent or very rare, but increasing grassiness could portend an increased likelihood of fire.

Many vegetation communities with a woody component, notably savannas and chaparral (including fynbos in South Africa), are fire-prone (Bond and Van Wilgen, 1996; van Wilgen, 2013). Surface fires are grass-fuelled and large plants (e.g. tall trees) may escape the effects of these fires by having thick bark and being tall enough to partly escape flames (Bond and Van Wilgen, 1996; Higgins *et al.*, 2000). Crown fires, usually occurring in forest or chaparral, occur when the leaf material of the woody plants themselves fuels the fire, and may result in near-complete mortality of woody plants in some systems (Stephens and Moghaddas, 2005). In the Karoo, it is unknown whether dwarf shrubs themselves can carry a fire, or are merely consumed within the flames of burning grass. The distinction is important in terms of the evolutionary development of the vegetation type (Paula and Pausas, 2008).

Following a fire, some woody plants, termed resprouters, have the ability to resprout from lignotubers, underground runners, or epicormic buds (Midgley, 1996), while others (nonsprouters) are killed and population recovery depends on seeds (Clarke *et al.*, 2010), which in the Karoo are typically present in the soil seedbank (Jones and Esler, 2004). The ability to resprout is apparently the ancestral condition in most plants, and the loss of the ability to resprout has been an evolutionary adaptation that confers benefit to nonsprouters (Bond and Midgley, 2003; Schwilk and Ackerly, 2005). In general, nonsprouters are larger and recruit more successfully from seed (Midgley, 1996), probably because resprouters need to invest more in carbohydrate storage to allow dormant buds to sprout and grow. Understanding the resprouting characteristics of Karoo plants may be necessary when developing appropriate post-disturbance management interventions (e.g. removal of animals) in conservation and agricultural systems, because nonsprouters recolonise from existing seedbanks, which in turn may be affected by grazing pressure (Milton, 1995).

Perennial grasses are generally well-adapted to survive fire as their meristems are close to the ground and are not likely to be killed by fire. This is particularly the case in humid grasslands where fire is an inherent feature of the landscape (Everson *et al.*, 1985). In drier systems, fire can induce tuft mortality (Zimmermann *et al.*, 2010) but may still maintain ecosystem structure and functioning (Humphrey, 2015). Fire in semi-arid grasslands adjacent to the eastern Karoo can induce tuft mortality and reduce grass production, and fire is often discouraged on this basis (Snyman, 2004). Accordingly, it is anticipated that grasses in the semi-arid eastern Karoo would be negatively impacted in some way by fire, probably incurring some level of mortality.

This paper describes the effect of a single fire on vegetation structure and composition of a grassy dwarf-shrubland in the eastern Karoo. We addressed two questions: 1) what is the mortality response of individual species to fire and 2) what are the effects of fire on vegetation structure and composition? To our knowledge, this is the first published report of the responses of grassy Karoo vegetation communities to fire.

7.2 Methods

Boesmanskop (31° 26.004'S 25° 1.645'E) is a section of the research farm of the Grootfontein Agricultural Development Institute (GADI), incorporating a 40 m high, flat-topped hill, and from an agricultural perspective represents veld in excellent condition (du Toit, 2002b). The area is a typical Karoo grassy shrubland, but there are some scattered trees and large shrubs on the slopes of the hill. Mean annual rainfall from 1889-2013 is 374 mm (range = 118-731 mm), but over the past 20 years has been higher (445 mm, range = 193-727 mm) (du Toit, 2010). Geology is of the Katberg Formation of the Tarkastad Subgroup, with level valley floors of Quaternary alluvial deposits, and hills predominantly of sandstone (Groenewald, 2011). There are no records from the past century of the area having burnt.

At approximately 16:00 on 26 September 2012 an accidental wildfire was ignited near Boesmanskop (Figure 7.1). The cause of the fire is unknown, but it began next to the highway so presumably was anthropogenic, perhaps arising from a spark or cigarette. It burnt with the prevailing wind in a south-easterly direction, increasing in width, and consuming the south-western portion of the hill. Part of the fire front extinguished itself upon reaching roads to the west and south, and the rest of the fire was extinguished manually. The total area burnt was 24.3 ha.

There had been no rain for the preceding nine days, and only 1 mm of rain over the two weeks before that. Over the preceding winter there had been approximately 75 frosty nights, ensuring that all grass leaves were 100% cured (*sensu* Cheney and Sullivan, 2008). Temperatures earlier during the afternoon of the fire had reached 31°C, and 28°C the previous day. Although not measured, temperature at the time of the fire was estimated at about 25°C. Relative humidity was very low (10%), indicating very dry conditions, which would be conducive to a fire being ignited from any incidental spark (Cheney and Sullivan, 2008). Because the rate of spread of the fire was not measured, or calculated with any confidence from weather data, fire intensity could not be calculated. One week after the fire, the exact boundary of the burnt area was delineated on foot using a global positioning system (GPS).

Six sites, representing the structural and compositional diversity of the area, were selected to compare burnt with unburnt veld over a topgraphic gradient (Figure 7.1). Sites 1 and 2 are Karoo flats, sites 3 and 6 are hill slopes, and sites 4 and 5 are on hilltop. For statistical purposes, sites are considered independent as they are spatially unconnected, and the final position of the fire line is randomly positioned in that the fire passage was not determined by vegetation but rather by the direction of the wind. The area has been grazed by sheep and cattle at relatively low stocking rates for over a century (0.056 AU.ha^{-1} since 1991).

Vegetation sampling was conducted from 30 April to 6 May 2013, about seven months after the fire and at the end of the growing season in the area. To describe the structure and composition of shrubs, five 5 x 15 m quadrats were sampled on the burnt and unburnt sections at each site and the dimensions (height, width, and length) and species of all shrubs (> 0.2 m) were recorded. To describe overall vegetation composition (i.e. including grasses and other small plants), the cover of all vascular plant species found within each of twelve 1 x 1 m quadrats on each of the burnt and unburnt sections at each of the six sites was described using the Domin scale, and values were converted to a percentage (Jager and Looman, 1987). The sampling intensity was chosen because species/area curves for the sites generally became asymptotic after between 3 and 10 quadrats, and while new species were still encountered beyond the tenth quadrat, these were typically rare and contributed very little to total cover. Quadrats were positioned to exclude the large trees and shrubs occurring on the hill slopes. Additionally, the burnt area was traversed on foot and all species not encountered during the quadrat surveys were recorded. To measure grass biomass, all grass within five 1x1 m quadrats on the burnt and unburnt sections at each of the sites was clipped to a height of approximately 2 cm. Grass was then separated into green and brown fractions, oven dried to constant weight at 60°C for 72 hours, and weighed.

Species were defined as fire tolerant if they were growing in the burnt area and were obviously not a seedling, i.e. remnants of the old plant were visible. Growth forms included woody plants, succulents, ferns, grasses, perennial herbs, and perennial herbaceous geophytes. While evidence of an old plant was sometimes lacking for the geophytes, they were assumed to be fire tolerant as geophytes by definition regrow from underground storage organs following above-ground defoliation (Pausas *et al.*, 2004). Species were defined as being fire sensitive if they a) were absent in burnt areas and b) occurred in enough unburnt quadrats to be statistically more abundant in unburnt than burnt areas; this was tested using logistic regression with sites as replicates (reference cell coding approach; Quinn and Keough, 2002). Species were defined as having an unknown response to fire if they did not fit into either of the previous categories.

Canopy cover of a shrub was calculated as an ellipse (Equation 7.1). Total shrub cover per quadrat was determined as the sum of the areas of the individual shrubs.

$$A = \frac{\pi x y}{4} \qquad \text{Equation 7.1}$$

Where A = area and x and y width and length.

Average shrub height, percent cover, and grass biomass were compared using paired t-tests. Shrub composition on burnt and unburnt areas was compared using a Blocked Multi-Response Permutation Procedure (BMRPP), using Euclidean distances to measure composition differences (Mielke, 1991). This procedure is sensitive to the absolute rather than the relative abundance of species and was used because of the low occurrence of shrubs in the burnt fractions. After removing percentage bare ground and rocks as pseudo-species, other compositional data were described using non-metric multidimensional scaling (NMMS) using the software packages WinKyst (Šmilauer, 2002) and CANOCO (Ter Braak and Šmilauer, 2002) . Total numbers of species and plants were compared using a Chi-square test.

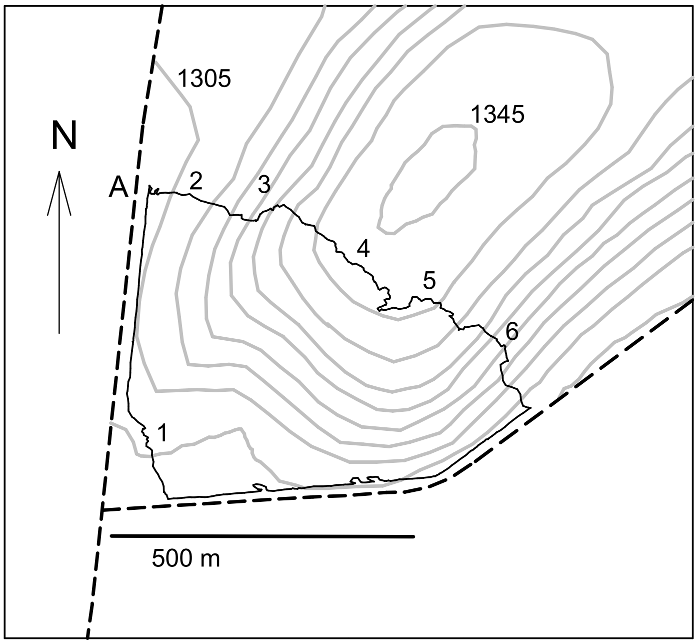


Figure 7.1 Location of the Boesmanskop fire at Grootfontein. Dotted lines are roads, grey lines are contours in m a.s.l. (5 m intervals), the black line delineates the burnt area, numbers 1-6 are survey sites (see text), and "A" is the ignition point.

7.3 Results and discussion

A total of 108 species from 74 genera and 29 families was found. All but two species (ferns) were angiosperms, of which 79 were dicotyledons and 27 monocotyledons. Of the monocotyledons, 17 species were grasses. Four species were annuals, two were biennials, and the remaining 102 species were perennial. Two exotic species, the annual herb *Conyza bonariensis*, and the biennial herb *Tragopogon porrifolius*, were encountered.

7.3.1 Response of species to fire

Ninety of the 108 species were found in either or both the small and large quadrats, and a further 18 species, including the four large shrub or tree species excluded from the quadrat surveys, were revealed in the search of the burnt area (Table 7.1). Seventy four species were confirmed to be fire-tolerant, including all grass species, four geophytes, and two ferns; the remaining species were woody plants or succulents, including the four species of large shrubs or trees. There were six fire sensitive species, all of which were dicotyledons from the families

Asteraceae (*Eriocephalus*), Aizoaceae (*Ruschia*), Crassulaceae (*Crassula*), and Geraniaceae (*Sarcocaulon*). Two of these genera comprised two species: *Eriocephalus ericoides* and *Eriocephalus spinescens*, and *Crassula muscosa* and *Crassula subaphylla*. Extirpation of these species indicates that fire acts as a disturbance, in that it is a discrete event that initiates succession at some spatial scale (Collins *et al.*, 1995). Burnt remains of *Eriocephalus* species, *Ruschia intricata*, and *Sarcocaulon salmoniflorum* were abundant and could be positively identified and confirmed to have not resprouted after the fire. There were no confirmed cases of congenerics having differing responses to fire (i.e. a genus with both fire-tolerant and fire-sensitive species), but all fire-sensitive species had fire-tolerant confamilials. This is not unexpected, as taxonomy is not necessarily a predictor of mortality response to fire. For example, some species of *Erica* in South African fynbos contain both seeder and resprouters phenotypes (Ojeda *et al.*, 2000). Twenty-eight species had an unknown response to fire, and were typically rare, non-perennial, or herbaceous.

The Boesmanskop fire revealed clear evidence of both sprouter and non-sprouter responses to fire. The number of sprouter relative to non-sprouter species was high, which would be expected in vegetation that experiences fires infrequently where, in contrast, fire-prone systems with both life forms present often include a high number of seeder species (Ojeda *et al.*, 2000). In the succulent Karoo, which does not experience fire, Rahlao *et al.* (2009) found only two species capable of resprouting after being burnt in a fire enabled through artificial fuel loads. The fire-sensitive species at Boesmanskop reflected a range of growth forms: *C. muscosa* is a succulent herb, *C. subaphylla* and *R. intricata* are dwarf shrubs with succulent leaves, *Sarcocaulon salmoniflorum* is a succulent shrub with thick, flammable stems and non- or slightly-succulent leaves, and the *Eriocephalus* species are both large, non-succulent dwarf shrubs. For each of these growth forms there are other species that were fire-tolerant.

A general pattern at Boesmanskop was that congenerics had similar responses to fire. All *Asparagus* species (6), all woody *Hermannia* species (6), all *Pentzia* species (4) excluding the rare *P. spinescens* (unknown response; 4 plants), and all *Helichrysum* species (3) excluding the rare *H. lucilioides* (unknown response; 1 plant) were fire tolerant. Both of each the *Eriocephalus* and *Crassula* species were fire-sensitive, and no species of the *Pteronia* genus (although these were comparatively rare) were found in the burnt section.

For a non-sprouter to survive a fire, it must recruit from seed. In fire-prone systems, heat (e.g. Herranz *et al*., 1998) or smoke (Crosti *et al.*, 2006) from the fire may break seed dormancy and encourage germination. The converse can also be true – for example, ash residues that increase soil pH can act as a germination inhibitor (Henig-Sever *et al.*, 1996). At Boesmanskop, no seedlings of any of the fire-sensitive species were found, this despite a season of good rainfall and the removal of all livestock.

Table 7.1 List of species at Boesmanskop arranged according to a) response to fire and b) growth form. Asterisks reflect in which surveys they were found: Q = found in 1x1 m quadrats, S = found in 5x15 m quadrats, F = found in a search of the burnt area

Species with Authority	Q	S	F
Fire sensitive species (nonsprouters)			
Perennial dwarf shrubs			
Eriocephalus ericoides (L.f.) Druce	*	*	
Eriocephalus spinescens Burch.	*	*	
Perennial succulent dwarf shrubs			
Crassula subaphylla (Eckl. & Zeyh.) Harv.	*		
Ruschia intricata (N.E.Br.) H.E.K.Hartmann & Stüber	*	*	
Sarcocaulon salmoniflorum Moffett	*	*	
Perennial succulent herb			
Crassula muscosa L.	*		
Fire tolerant species			
Perennial dwarf shrub (resprouters)			
Amphiglossa triflora DC.		*	*
Asparagus crassicladus Jessop			*
Asparagus striatus (L.f.) Thunb.	*		
Chrysocoma coma-aurea L.	*		
Felicia filifolia (Vent.) Burtt Davy	*	*	*
Felicia muricata (Thunb.) Nees	*	*	*
Helichrysum dregeanum Sond. & Harv.	*	*	*
Helichrysum rutilans (L.) D.Don	*		
Helichrysum zeyheri Less.	*	*	*
Hermannia cuneifolia Jacq.			*
Hermannia desertorum Eckl. & Zeyh.	*		
Hermannia filifolia L.f.	*	*	
Hermannia multiflora Jacq.	*		
Hermannia pulchella L.f.	*		
Hermannia spinosa E.Mey. ex Harv.	*	*	*

Species with Authority	Q	S	F
Melolobium microphyllum (L.f.) Eckl. & Zeyh.	*	*	*
Nenax microphylla (Sond.) Salter	*	*	*
Osteospermum leptolobum (Harv.) Norl.		*	*
Pegolettia retrofracta (Thunb.) Kies	*	*	*
Pelargonium ramosissimum (Cav.) Willd.		*	*
Pentzia globosa Less.	*	*	*
Pentzia incana (Thunb.) Kuntze	*		*
Pentzia pinnatisecta Hutch.			*
Pentzia sphaerocephala DC.	*	*	*
Phymaspermum aciculare (E.Mey. ex Harv.) Benth. & Hook. Ex B.D. Jacks.			*
Phymaspermum parvifolium (DC.) Benth. & Hook. Ex B.D.Jacks.	*		*
Rosenia humilis (Less.) K.Bremer	*		*
Salsola calluna Fenzl ex C.H.Wright			*
Selago saxatilis E.Mey.	*		
Stachys rugosa Aiton	*	*	*
Wahlenbergia albens (Spreng. Ex A.DC.) Lammers		*	*
Wahlenbergia tenella (L.f.) Lammers	*		*
<u>Perennial parasitic dwarf shrub (resprouters)</u>			
Thesium hystrix A.W.Hill	*	*	*
<u>Perennial shrubs (resprouters)</u>			
Asparagus africanus Lam.	*		
Asparagus mucronatus Jessop			*
Asparagus retrofractus L.			*
Asparagus suaveolens Burch.			*
Lycium cinereum Thunb.	*	*	*
<u>Perennial succulent dwarf shrubs (resprouters)</u>			
Hertia pallens (DC.) Kuntze			*
Pachypodium succulentum (L.f.) Sweet			*
Sarcostemma viminale (L.) R.Br.	*		
Tylecodon ventricosus (Burm.f.) Tölken	*		
Bulbine frutescens L.			
<u>Perennial succulent shrubs (resprouters)</u>			
Euphorbia mauritanica L.			*
<u>Perennial trees/ large shrubs (resprouters)</u>			
Buddleja saligna Willd.			*
Diospyros austro-africana De Winter			*
Euclea undulata Thunb.			*
Searsia erosa (Thunb.) Moffett			*

Species with Authority	Q	S	F
Perennial ferns (resprouters)			
Cheilanthes eckloniana (Kunze) Mett.	*		*
Pellaea calomelanos (Sw.) Link			*
Perennial succulents			
Mestoklema tuberosum (L.) N.E.Br. ex Glen		*	*
Trichodiadema pomeridianum L.Bolus	*		
Perennial grasses			
Aristida congesta Roem. & Schult.	*		*
Aristida diffusa Trin.	*		*
Cymbopogon pospischilii (K.Schum.) C.E. Hubb.	*		*
Digitaria eriantha Steud.	*		*
Enneapogon scoparius Stapf	*		*
Eragrostis bicolor Nees	*		*
Eragrostis curvula (Schrad.) Nees	*		*
Eragrostis curvula var conferta Stapf	*		*
Eragrostis lehmanniana Nees	*		*
Eragrostis obtusa Munro ex Ficalho & Hiern	*		*
Eustachys paspaloides (Vahl) Lanza & Mattei	*		*
Heteropogon contortus (L.) Roem. & Schult.	*		*
Oropetium capense Stapf	*		*
Sporobolus fimbriatus (Trin.) Nees	*		*
Tetrachne dregei Nees	*		*
Themeda triandra Forssk.	*		*
Tragus koelerioides Asch.	*		*
Perennial herbs			
Gazania jurineifolia			*
Perennial herbs (geophytes)			
Cyperus capensis (Steud.) Endl.	*		*
Moraea pallida (Baker) Goldblatt			*
Oxalis spp	*		*
Pelargonium aestivale E.M.Marais			*
Unknown response to fire			
Perennial dwarf shrubs			
Gnidia polycephala (C.A.Mey.) Gilg	*		
Helichrysum lucilioides Less.		*	
Pelargonium abrotanifolium (L.f.) Jacq.		*	
Pentzia spinescens Less.		*	
Pteronia glauca Thunb.		*	

Species with Authority	Q	S	F
Pteronia sordida N.E.Br.		*	
Pteronia tricephala DC.		*	
Selago geniculata L.f.	*	*	
Solanum tomentosum L.			*
Perennial herbs			
Commelina africana L.	*		
Hermannia depressa N.E.Br.			*
Hermannia pulverata Andrews	*		
Indigofera alternans DC.	*		
Jamesbrittenia pinnatifida (L.f.) Hilliard	*		
Launaea rarifolia (Oliv. & Hiern) Boulos			*
Pollichia campestris Aiton		*	*
Salvia verbenaca L.	*		
Annual or biennial herbs			
Arctotheca calendula L.			*
Conyza bonariensis (L.) Cronquist	*		
Geigeria filifolia Mattf.	*		
Hermannia coccocarpa (Eckl. & Zeyh.) Kuntze	*		
Lepidium africanum (Burm.f.) DC.	*		
Pelargonium minimum (Cav.) Willd.	*		
Tragopogon porrifolius L.	*		
Perennial succulents			
Rabiea albinota (Haw.) N.E.Br.	*		
Perennial succulent dwarf shrub			
Adromischus maculatus (Salm-Dyck) Lem.	*		
Perennial succulent herbs			
Anacampseros filamentosa (Haw.) Sims	*		
Senecio radicans (L.f.) Sch.Bip.	*		

7.3.2 Shrub survey

Unburnt sites were uniformly dominated by *Eriocephalus ericoides*, but varied along an altitudinal gradient according to the presence of other sub-dominant shrub species (Figure 7.2). Composition of the Karoo flats was characterised by *Felicia muricata* and *Selago geniculata*, hill slopes by *Stachys rugosa* and the hill top sites by *Ruschia intricata*. In the burnt area there were significantly fewer shrubs at least 0.2 m in height (χ^2=512, df=1, P<0.0001), and significantly fewer species (χ^2=8.39, df=1, P=0.0038), than in the unburnt area (Table 7.2). Species richness across the six sites was lower in the burnt section, and there were no abundant species common to both burnt and unburnt portions. Accordingly, species composition was significantly different (P=0.008 using BMRPP) between the burnt and unburnt areas. Most shrubs in the burnt section were *Stachys rugosa*, an unpalatable species (Botha *et al.*, 2001) that regrows rapidly following disturbance. Both the average height and canopy cover of shrubs in the burnt section were significantly lower than in the unburnt section, and the total shrub cover in the unburnt section (Figure 7.3) was starkly higher than in the burnt section (Figure 7.4). The net effect of the fire, therefore, was to completely change the structure and composition of the > 0.2 m shrub component. Comparing this to the effects of high-intensity fires in savanna systems (Bond and Van Wilgen, 1996), the response of the vegetation at Boesmanskop was similar in that most of the woody species resprouted, and will presumably regrow. It differs from savanna systems in that some species, including the most common species, were extirpated.

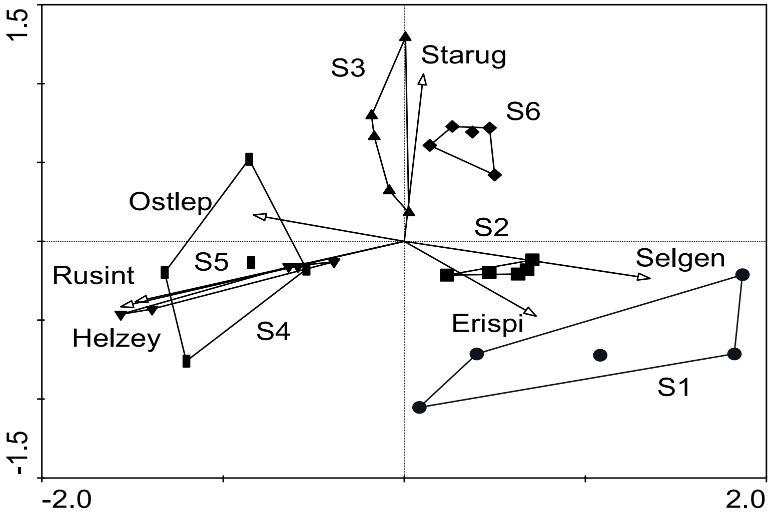


Figure 7.2 Non-metric multidimensional scaling (NMS), rotated by principal components analysis (PCA), of Bray-Curtis distances among unburnt sites based on abundance of species of shrubs. Stress = 0.161. Overlaid are species trends (arrows) across the NMS (species with low variability in the ordination are not shown). Starug = *Stachys rugosa*, Selgen = *Selago geniculata*, Erispi = *Eriocephalus spinescens*, Helzey = *Helichrysum zeyheri*, Rusint = *Ruschia intricata*, Ostlep = *Osteospermum leptolobum*.

Figure 7.3 Photograph of unburnt vegetation, taken perpendicular to the ground, approximately 30 m SE of Site 3 at Boesmanskop. Grass cover (much of it dead leaves) is high, with virtually no bare ground visible. Two *Eriocephalus ericoides* plants are visible toward the top of the photograph.

Figure 7.4 Photograph of burnt vegetation, taken perpendicular to the ground, approximately 30 m SE of Site 3 at Boesmanskop. Grass cover (much of it green leaves) is low, with bare ground clearly visible. A dead *Eriocephalus ericoides* plant is visible toward the top-right of the photograph.

Table 7.2 Statistics of shrub populations (>0.2 m height) on burnt and unburnt veld at Boesmanskop. RA = relative abundance (%), asterisks indicate significant differences between values in that row at P<0.01(**) or P<0.001(***)

Parameter	Burnt	Unburnt
Total number of species**	12	31
Average number of species per site***	3.00	9.83
Total number of plants***	170	916
Average height of plants (m)**	0.305	0.380
Average canopy area per plant (m^2)***	0.129	0.691
Average shrub canopy cover (%)**	0.80	23.0
Most abundant species (RA)	*Stachys rugosa* (55%)	*Eriocephalus ericoides* (32%)
Second most abundant species (RA)	*Wahlenbergia albens* (16%)	*Ruschia intricata* (15%)
Third most abundant species (RA)	*Pegolettia retrofracta* (6%)	*Selago geniculata* (11%)

7.3.3 Overall composition survey

Percentage bare ground was significantly (t=6.41, d.f.=5, P=0.0014) higher in the burnt (44.9%) than the unburnt fraction (28.7%), indicating that vegetation cover had not returned to its pre-burn levels. Grass cover declined significantly (t=2.76, d.f.=5, P=0.020) but relatively little (48.2% to 41.1%) compared to the large decrease in the perennial Karoo shrub component, which declined significantly (t=4.6, d.f.=5, P=0.002) from 16.6% to 2.6%. This may indicate that the fire has conferred a competitive advantage to grasses over Karoo shrubs, and future fires may further constrain or reduce shrub productivity (Roques *et al.*, 2001), resulting in a shift to increased grassiness. Such a process may be reversed if rainfall decreases enough that grasses cannot produce sufficient biomass to support fire.

The overall composition between the unburnt sites showed some variation, which was associated mainly with the abundance of large, perennial, palatable grass species (Figure 7.5a). The relatively unpalatable and sometimes invasive (Botha *et al.*, 2001) succulent shrub *Ruschia intricata* characterised the hilltop sites. Interestingly there was no evident separation of composition between burnt and unburnt sites (Figure 7.5b), indicating that species composition (as opposed to the relative abundance of growth forms describe earlier) after the fire was similar to that before the fire. This is because most species resprouted after the fire. This suggests that a single fire does not induce a major compositional shift in vegetation of the eastern Karoo, unlike the effects that a drought may cause (Milton and Hoffman, 1994; O'Connor and Roux, 1995), or long-term heavy grazing (Seymour *et al.*, 2010). It is anticipated that post-fire succession, therefore, starts from a state very similar to the starting state, described as "initial floristic composition" by Egler (1954) *sensu* "All the species that are likely to be involved in a succession are present at the beginning, though some are predominant early on, and others later…" (Wilson *et al.*, 1992). An ingress of early successional species was absent at Boesmanskop, despite gaps being made available through the reduction in shrub cover, although they have been found in other Karoo systems (Esler *et al.*, 2006).

This study does not reveal whether the extirpated shrub species will re-colonise, or at what rate. No seedlings were found seven months after the fire, but seed germination may be an infrequent process in Karoo regions, and may be influenced by the timing of rainfall (Milton, 1995). While it may be expected that herbivory, particularly by sheep (Tiver and Andrew, 1997; Tiver *et al.*, 2001) would decrease the chance of survival of woody seedlings, there is evidence that this might not be the case in the Karoo, and that rainfall and competition by other plants may play larger roles (Milton, 1994, 1995).

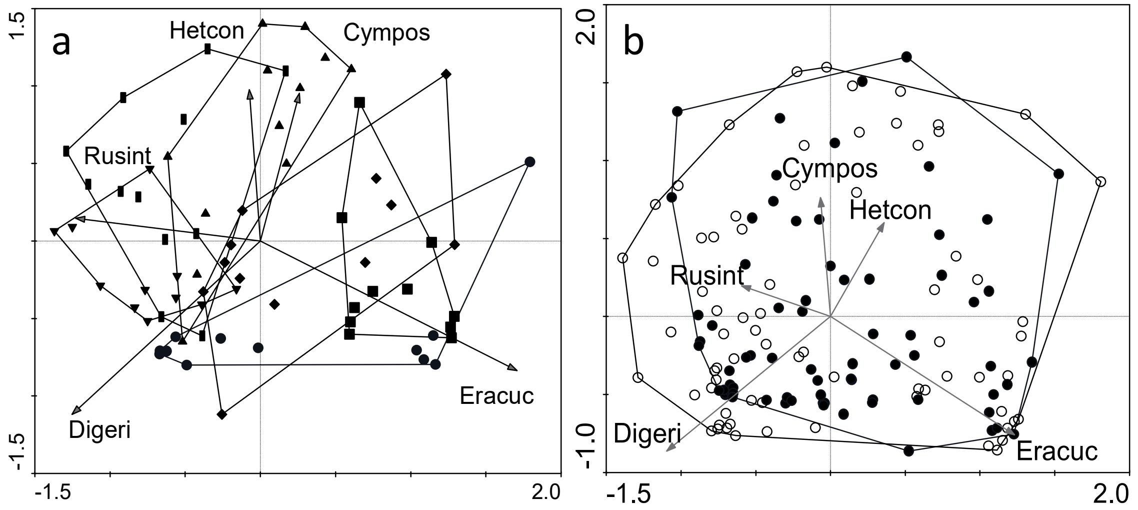


Figure 7.5 Non-metric multidimensional scaling (NMS), rotated by principal components analysis (PCA), of Bray-Curtis distances among (a) unburnt sites and (b) burnt and unburnt sites, based on abundance of all species. Stress = (a) 0.228 and (b) 0.225. Overlaid are species trends (arrows) across the NMS (species with low variability in the ordination are not shown). Symbols are (a) Site 1 (●), Site 2 (■), Site 3(▲), Site 4 (▮), Site 5 (▼), and Site 6 (◆), and (b) burnt (●) and unburnt (○) sites. Digeri = *Digitaria eriantha*, Rusint = *Ruschia intricata*, Hetcon = *Heteropogon contortus*, Cympos = *Cymbopogon pospischilii*, Eracuc = *Eragrostis curvula* subsp *conferta*.

7.3.4 Grass biomass

Grass biomass on the unburnt fraction, measured after seven months of absence from grazing, was 1.79 $t.ha^{-1}$, which was significantly higher than the regrowth on the burnt fraction (0.65 t/ha) ($t=-4.15$; $df=5$; $P=0.014$), while the green fraction was significantly higher on the burnt fraction (0.65 t/ha) than on the unburnt fraction (0.13 t/ha) ($t=8.64$; $df=5$; $P<0.0001$). The pre-burn fuel load was therefore probably less than 1.79 $t.ha^{-1}$, which would mean that the fire intensity was likely to have been relatively low. The fire removed grass that would have been available as livestock fodder, although the higher proportion of green material in the regrowth may have been of a higher quality than the original material (van der Vijver *et al.*, 1999). One would anticipate from these results that, in the short term at least, the potential for livestock production off the veld (carrying capacity) would have decreased, that performance per animal would not decline, and that the vegetation structure is possibly more suited to cattle production than to sheep production, as cattle are bulk grazers while sheep utilize grass but also browse Karoo shrubs.

7.4 Conclusion

Most species at Boesmanskop appear to be resprouters, although there is evidence of obligate seeders, suggesting that the vegetation of the eastern Karoo may be relatively resilient to fire. However, the fire did cause a significant change in the shrub structure of the vegetation, and the composition of fast-growing resprouters did not resemble that of the original composition. Importantly, the most abundant shrub was extirpated in the fire. Grasses recovered quickly after the fire, which may have conferred a competitive advantage to them, implying that future fires may further increase grassiness. Of future interest will be the patterns of colonization of the bare areas following the extirpation of shrubs, mainly *E. ericoides*. The Boesmanskop fire is now the site of a long-term monitoring programe at Grootfontein, as are other fires in the Karoo that have since occurred. This research provides novel insight into fire-plant dynamics in the eastern Karoo, and provides some background for 1) how to manage this vegetation after an accidental fire and 2) how some shrub species, notably *Ruschia*, might be controlled with fire.

CHAPTER 8 PHOTOGRAPHIC EVIDENCE OF FIRE-INDUCED SHIFTS FROM DWARF-SHRUB- TO GRASS-DOMINATED VEGETATION IN NAMA-KAROO

8.1 Introduction

The Nama-Karoo is an inland biome in South Africa bounded by six other biomes: succulent Karoo (S and W), Albany thicket (SE), grassland (E), savanna (N), patches of desert (NW) and fynbos (SW). Rainfall ranges from <100 to >400 mm per year, with most of the biome receiving 200 mm or less (Cowling, 1986). Vegetation is characterised and dominated by perennial dwarf shrubs (some succulent) with perennial geophytes and shrubs, and perennial or annual grasses and herbs of varying abundance. The Nama-Karoo gives way to arid grassland along nearly its entire eastern flank. On the north-eastern boundary the transition from Nama-Karoo to grassland is gradual, while further south it is more abrupt, with Karroid vegetation on the lower-lying plains and grassland on the higher mountains (Mucina, Rutherford, *et al.*, 2006). The transition also occurs over a rainfall gradient, with the Nama-Karoo/ grassland boundary receiving between 380 and 450 mm (Zucchini and Nenadić, 2006), highlighting the importance of rainfall as a determinant of whether an area is Nama-Karoo or grassland (Mucina, Hoare, Lötter, *et al.*, 2006). Owing to high rainfall variability and periodic droughts, the Karroid and grassland conditions may fluctuate: (Acocks, 1953) noted that the eastern Nama-Karoo was “transitional, predominantly grassy, but fluctuating towards the Karoo condition during droughts”. There is evidence that such fluctuations have been a feature of parts of the Nama-Karoo/ grassland interface for 250,000 years, with Nama-Karoo replacing grassland during times of low rainfall (Mucina, Rutherford, *et al.*, 2006).

Almost all of the Nama-Karoo is grazed by livestock (mainly sheep and goats) and Acocks (1953) argued that the Nama-Karoo was expanding its original range, necessitating remedial agricultural practices by farmers, a view held by other authors and summarised by Roux and Theron (1987). However, in recent decades the eastern Nama-Karoo has become increasingly grassy, with the boundary of the Grassland Biome moving westwards (Hoffman and Cowling, 1990). The potential role that destocking has played in this has been advocated (Masubelele *et al.*, 2014), as has the possible influence of elevated rainfall from the mid-1970s (Hoffman and Cowling, 1990; du Toit, 2010; du Toit, van den Berg, *et al.*, 2015). A shift in seasonality of rainfall from late season to early season (du Toit and O’Connor, 2014) may also have promoted grassiness, because grasses are advantaged by rain falling in summer (O'Connor and Roux, 1995).

The importance of increased grassiness, and hence increased chance of fire, in arid and semi-arid landscapes, is well recognised. Invasive annual grasses in the deserts of the western United States have increased fire incidence (Esque *et al.*, 2004; Brooks and Matchett, 2006; Abatzoglou and Kolden, 2011; Lippitt *et al.*, 2013), and Rahlao *et al.* (2009) hypothesised a similar outcome in transitional Karoo invaded by *Pennisetum setaceum*. Grasses are significantly more tolerant of fire than shrubs are, and a combination of grass and fire has the ability to favour the development and persistence of grasslands over shrublands or forests, especially if fires are frequent (Bond, 2008). The duration of the effect of fire on community structure depends in part on the population biology and size of individuals of the woody component (Midgley, 1996). Where woody plants resprout following fire, or are large enough to survive the effects of the fire, then the effects may be relatively short-lived (Bond, 2008; Lamont *et al.*, 2011). Where woody plants are killed by fire (nonsprouters) then the effects of fire may be longer-lived because woody plants must re-establish from seed. For example, fynbos or chaparral may take about a decade to return to pre-fire structure (van Wilgen, 2013), while forests may take from several decades to a century (Geldenhuys, 1994; Paysen *et al.*, 2000). The grass layer in the Nama-Karoo rarely accumulates enough fuel to support a fire, especially in the arid west (Mucina, Rutherford, *et al.*, 2006), and fires typically occur only after several years of above-average rainfall (Palmer, 1990).

Despite its potential importance, the effects of fire on Nama-Karoo vegetation remain largely unexplored. Rahlao *et al.* (2009), at a site in the transition zone between Nama-Karoo and Succulent Karoo, found that most Karroid shrubs were killed by fires (generated using artificial fuel loads), recording only two species that were resprouters. du Toit *et al.* (2014) described vegetation responses at the Boesmanskop fire (Table 8.1), and found that 1) several species of dwarf shrub, including the co-dominants *Eriocephalus ericoides* and *Ruschia intricata*, were nonsprouters and hence locally extirpated by the fire, 2) 74 of the 108 species, including 38 species of dwarf shrub, were resprouters and 3) in terms of cover, there was a shift from grassy shrubland to grassland. It was predicted that nonsprouting shrubs would recolonise over time, allowing the vegetation to revert to grassy shrubland.

The objectives of this study were to exploit opportunities provided by a range of fires in the Karoo to test predictions made by du Toit *et al.* (2014) on a fire-induced biome switch, from Karoo shrubland to Karoo grassland, and its temporal persistence.

8.2 Methods

A dataset of fires that have burnt in the Nama-Karoo was developed. Information on the location of fires came from observations, historical research records, and satellite data (2000-2014) using FIRMS (Fire Information for Resource Management System) (NASA, 2014). The set is not exhaustive, but probably includes most large Nama-Karoo fires that have burnt since 2000 (Figure 8.1). All fire sites west of Middelburg in the Nama-Karoo (approximately 25°E) were visited between November 2014 and May 2015 and photographed (Table 8.1). The Boesmanskop and The Mills fires had previously been mapped by walking their perimeters using a GPS. This emerged to be an important factor for subsequent research: fire lines in the veld sometimes remain stark over time, while others become vague. Most of the Nama-Karoo fires identified between 2000 and 2014 occurred between 2010 and 2012, a period of particularly high rainfall (du Toit and O'Connor, 2014; du Toit, van den Berg, *et al.*, 2015). The sizes of the burnt areas were determined either from GPS records or estimated roughly using Google Earth imagery (Google, 2014). Fire extents of the Biesiespoort and Skietkuildam fires were underestimated as some of the satellite imagery predated the fires. Area burned ranged from 24 ha (Boesmanskop fire) to 1500 ha (Victoria West fire). Fires were not planned, and to the best of our knowledge all fires were actively extinguished, so it is likely that they would have been larger had there not been human intervention.

Table 8.1. Details of some known fires in the Nama-Karoo, 1976-2012, from west to east

Fire name	Location	Area (ha)	Year	Description
Inverness	31.3797° S 22.9172° E	1450	2012	Accidental ignition from discarded embers. Fire boundary photographed.
Jasfontein	31.5828° S 23.0526° E	504	2012	Lightning ignition. Photographed from a distance (not reproduced here).
Victoria West	31.4206° S 23.1641° E	1500	2011	Unknown ignition, probably from town. Fire boundary photographed.

Biesiespoort	31.6875° S 23.1962° E	>326	2008-2012	Unknown ignition. Photographed from a distance (not reproduced here).
Skietkuildam	31.8198° S 23.4744° E	>479	2011	Unknown ignition, possibly from highway. Fire boundary photographed.
Richmond	31.3673° S 24.0282° E	180	2010	Unknown ignition, possibly from highway. Fire boundary photographed.
De Aar	30.7010° S 24.0664° E	1007	2011	Unknown ignition, probably from town. Photographed from a distance (not reproduced here).
The Mills	31.1749° S 24.3727° E	1000	2011	Sparks from road construction crew. Fire boundary recorded using GPS; fire boundary photographed.
Middelburg Commonage	31.5219° S 24.9834° E	44	2010-2012	Unknown ignition. Fire boundary photographed.
Bangor	31.4236° S 25.0424° E	120	1976	Unknown ignition, possibly from highway. Section of burnt area photographed.
Boesmanskop	31.4355° 25.0250°	24	2012	Unknown ignition, probably from highway. Fire boundary recorded using GPS; fire boundary photographed (not reproduced here); detailed vegetation surveys conducted.

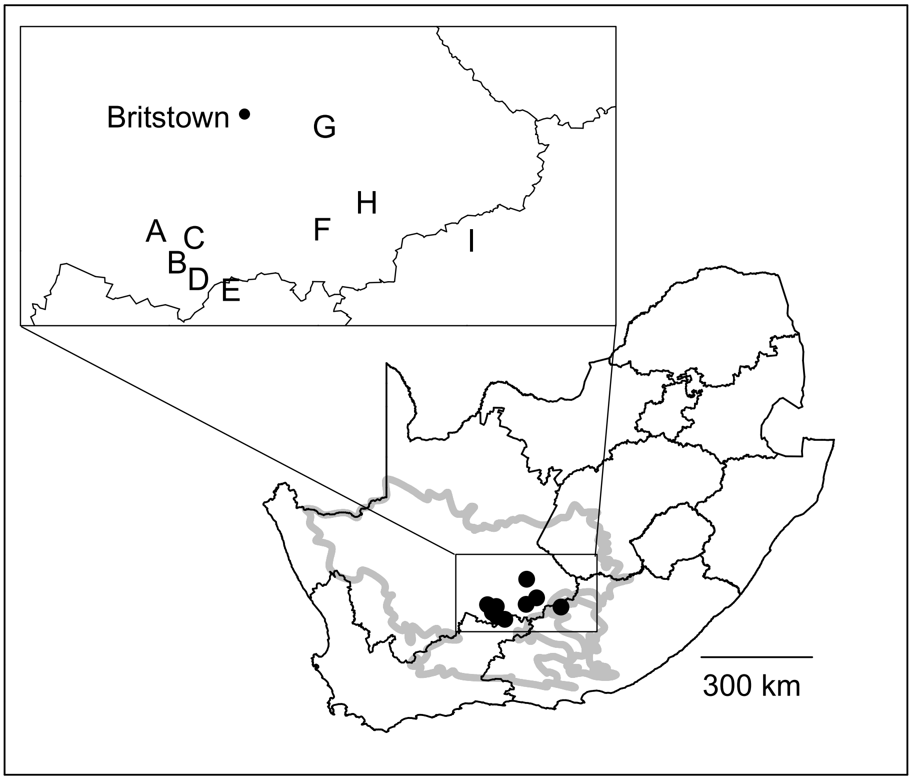


Figure 8.1. Location of all fires identified using Fire Information for Resource Management System (FIRMS), unless stated, in the Nama-Karoo west of Middelburg from 2000 to 2014. A: Inverness fire (2012), B: Jasfontein fire (2012), C: Victoria West fire (2011), D: Biesiespoort fire (between 2008 and 2012; not on FIRMS), E: Skietkuildam fire (2011), F: Richmond fire (2010), G: De Aar fire (2011), H: The Mills fire (2011), and I: Middelburg fires (not on FIRMS) –, Boesmanskop fire (2012), and Middelburg Commonage fire (2010-2012)). The grey line is the approximate perimeter of the Nama-Karoo Biome (Low and Rebelo, 1996). The Bangor fire (1976) is at the same site as the Middelburg fires.

8.3 Results

The general response to fire was a shift from a dwarf shrubland to open, often sparse, grassland with occasional dwarf shrubs, similar to the changes reported at the Boesmanskop fire (du Toit *et al.*, 2014). At The Mills fire there were striking examples of dense stands of *Ruschia intricata* (doringvygie) having been extirpated (Figure 8.2). Sites at the Mills (Figure 8.3), Inverness (Figure 8.4), Skietkuildam (Figure 8.5), Middelburg Commonage (Figure 8.6) and Richmond (Figure 8.7) fire sites all showed examples of the dominant *Eriocephalus ericoides* (kapokbos) being extirpated and veld shifting to open grassland. At the Victoria West (Figure

8.8) site the resprouter *Helichrysum dregeanum* was the dominant dwarf shrub, but although the species had resprouted after the fire, regrowth was minimal and the burnt area was structurally sparse grassland. The Victoria West site was clearly heavily grazed, which presumably contributed to the low biomass. In contrast, the resprouters *Salsola calluna*, *Chrysocoma ciliata*, *Pentzia globosa*, *Psilocaulon junceum*, *Euryops multifidus* and *Delosperma* spp. at a point on the Richmond fire site (Figure 8.7) in an ungrazed railway reserve had regrown to about half the size of their unburnt counterparts. The photograph of the veld burnt in the Bangor fire (Figure 8.9), which burnt in 1976, shows *Eriocephalus ericoides* as the dominant shrub.

Figure 8.2. Burnt (left) and unburnt (right) veld at The Mills site three years after the fire. Pictures are taken within 5 m of each other from opposite directions. Shrubs on the unburnt section are predominantly the nonsprouter *Ruschia intricata*.

Figure 8.3. Unburnt (left) and burnt (right) veld at The Mills site three years after the fire. Shrubs on the unburnt section are mainly the nonsprouter *Eriocephalus ericoides*.

Figure 8.4. Burnt (left) and unburnt (right) veld at the Inverness site two years after the fire. The nonsprouting *Eriocephalus ericoides* comprised about 20% of the shrubs.

Figure 8.5. Unburnt (foreground) and burnt veld at the Skietkuildam site three years after the fire. Most shrubs on the unburnt section are the nonsprouters *Eriocephalus ericoides*.

Figure 8.6. Unburnt (left) and burnt veld at the Middelburg Commonage site between two and four years after the fire. Most shrubs on the unburnt section are the nonsprouter *Eriocephalus ericoides*.

Figure 8.7. Ungrazed veld burnt (left) and unburnt at the Richmond site four years after the fire. On the unburnt section the dominant shrub is the nonsprouter *Eriocephalus ericoides*. Shrubs that have resprouted on the burnt section include *Salsola calluna*, *Chrysocoma ciliata*, *Pentzia globosa*, *Psilocaulon junceum*, *Euryops multifidus* and *Delosperma* spp.

Figure 8.8. Burnt (left) and unburnt veld at the Victoria West site three years after the fire. Grey bushes on the burnt section are the resprouter *Asparagus suaveolens* and dark bushes on the unburnt section are predominantly the resprouter *Helichrysum dregeanum*.

Figure 8.9. Veld near Middelburg that was reportedly burnt in 1976. The nonsprouting *Eriocephalus ericoides* is the dominant shrub species.

8.4 Discussion

8.4.1 Temporal effect of a single fire

The effect of a single fire is likely not permanent because many shrub species resprout, and nonsprouters eventually recolonise following a fire. There is evidence for this at the Bangor fire site where veld burnt in 1976 is today well-populated with the nonsprouter *Eriocephalus ericoides* (Figure 8.9). Recurrent fire, however, may induce a permanent shift to arid grassland because fire can eliminate nonsprouters by exhausting their seedbank (van Wilgen, 2013), although the seedbank of well-dispersed species, such as the wind-dispersed *Eriocephalus ericoides* (Esler *et al.*, 2006), may be replenished from adjacent areas. The fire frequency necessary to eliminate nonsprouters in the Nama-Karoo is not known but *Eriocephalus* is producing seed at the Grootfontein 1976 fire site (39 years later), and probably has been for many years. Therefore a fire return interval of greater than 40 years (maybe 20 or 30) is unlikely to eliminate *Eriocephalus*. Interestingly, there were no *Eriocephalus* seedlings at the Boesmanskop fire site, despite two subsequent seasons of good rains (du Toit and O'Connor, 2014), and none were evident at any of the sites visited during this study. The population biology of Nama-Karoo plants as a key knowledge gap has long been recognised (Cowling and Roux, 1987) and will limit our understanding of Nama-Karoo vegetation dynamics, and needs to be addressed.

8.4.2 Fire and the boundary of the Nama-Karoo

At all the sites visited in this study, fire induced a shift from the Karroid condition to sparse grassland (albeit arguably temporary). Importantly, this shift occurs simply through the removal (mortality or topkill) of dwarf shrubs, and the survival and probable faster regrowth of grasses. A shift from Nama-Karoo to grassland does not require the recruitment of other species or life-forms. Thus, fire in the Nama-Karoo at the Nama-Karoo/ grassland boundary would, through the process of the removal of dwarf shrubs, have the effect of the grassland 'encroaching' into the Nama-Karoo. This raises the question of whether other biomes would 'encroach' into the Nama-Karoo Biome in the event of fire at their common boundaries, and it is surmised that they probably would not. Succulent Karoo and Nama-Karoo Biomes are separated according to rainfall seasonality and soil type (Mucina, Norbert Jürgens, le Roux, *et al.*, 2006). Vegetation is sparse in the Desert Biome (Jürgens, 2006), and is unlikely to support fire. However, were fire to occur, grasses would need to be extirpated to form desert (otherwise it would remain arid grassland), but grasses are generally tolerant of fire, certainly in the eastern Nama-Karoo (du Toit *et al.*, 2014). The Nama-Karoo/ savanna boundary appears to be reliant on geological and edaphic factors, which would not be influenced by fire (Mucina, Rutherford, *et al.*, 2006). Expansion of Albany Thicket can occur, depending on disturbance regime, (Mucina, Rutherford, *et al.*, 2006), but expansion into the Nama-Karoo Biome is probably prevented by frost (Duker, Cowling, du Preez, Vyver, *et al.*, 2015). It is difficult to speculate on whether fynbos would encroach burnt Nama-Karoo, and the two biomes share a very limited boundary and occupy different edaphic environments. Therefore, the occurrence of fire, allowed by elevated rainfall, as a process whereby a biome can encroach into the Nama-Karoo appears to be unique to the Grassland Biome. In areas not associated with the Nama-Karoo/ grassland boundary, fire in the Nama-Karoo would merely result in patches of sparse grassland forming.

8.4.3 Practicalities of fire research in the Nama-Karoo

It is noteworthy that these insights into the effects of fire on Nama-Karoo vegetation did not come about through planned experiments but rather from observations that were made opportunistically and in the absence (at least at the beginning) of an *a-priori* research question. Controlled burning of Nama-Karoo veld has seemingly never been conducted, despite its potential importance having been recognised (Cowling and Roux, 1987). Part of the problem with undertaking research may be that research facilities in the Nama-Karoo are not familiar with the practical aspects of applying controlled burns. More important may be that controlled burns would (for legal and policy reasons) necessarily have to be conducted under moderate climatic conditions, and the behaviour of such fires can be very different from the fires burnt under extreme conditions (Cheney and Sullivan, 2008), which is usually when accidental fires occur. Indeed it is likely that fires will occur only under extreme climatic conditions (notably high wind speeds) if fuel loads are relatively sparse. Accidental fires, therefore, offer opportunities for research that planned experiments would unlikely be able to emulate.

8.5 Conclusion

The recent Nama-Karoo fires allow us some insight into a factor, hitherto accorded little attention, that may convert Nama-Karoo to grassland or alter the position of the Nama-Karoo/

grassland boundary. The findings will be of particular importance should grassiness in the Nama-Karoo prevail or increase. Conditions favouring increased grassiness include reduced stocking rates of livestock, increased rainfall, and a shift to early-season rainfall. To determine the effect of fire in the Nama-Karoo requires monitoring of grassiness across the biome (for example using satellite imagery), careful recording of the spatial characteristics of fires when they occur, and ongoing monitoring of vegetation thereafter. Additionally, the population biology of Karroid plants is a knowledge gap and requires attention.

CHAPTER 9 DISCUSSION AND CONCLUSION

This section starts with concise answers to the questions initially posed in the thesis. This is followed by a general discussion of the work presented, followed by some ideas on how these findings might be incorporated into an existing model of functioning of Karoo vegetation (Milton and Hoffman, 1994). Following this are comments on implications of the research in terms of Karoo management and, last, some thoughts on the directions for future research.

In this section, reference is made to various images of the Karoo presented in the appendix to provide visual context for the reader.

9.1 Brief answers to the questions posed

Question 1: What have been the patterns of rainfall cyclicity and directional change at Grootfontein, and how might these have influenced composition and productivity?

> ***Answer to Question 1:*** *There is clear evidence of rainfall cyclicity at approximately 20 and approximately 60 years. Directional changes are evident at the period of these cycles, and rainfall has been high since the mid-1970s. These results are consistent with the general observation of increasing grassiness in the Karoo, coupled with increased productivity especially from grass.*

Question 2: How do rainfall and grazing, alone and in interaction, influence vegetation composition in the eastern Karoo?

> ***Answer to Question 2:*** *Increased rainfall results in an increase in perennial plant cover, predominantly that of grasses. Recent high rainfall supports the hypothesis that increased rainfall shifts vegetation from a Nama-Karoo state to a Grassland state. Nama-Karoo vegetation can sustain grazing at recommended stocking rates (1 LSU per 9 ha), but if grazing is concentrated in the summer months then grasses decline and shrubs may increase. Under conditions of continued high rainfall, grass establishment and growth will occur despite the presence of even heavy summer grazing. Under drought conditions,*

grass populations (and occasionally shrub populations) can collapse despite lenient grazing.

Question 3: What have been the trends in minimum temperatures, frost, and potential growth season at Grootfontein, how might these have influenced botanical composition and productivity, and is there evidence of increasing temperatures as occur with global warming?

> ***Answer to Question 3:*** *Minimum temperatures and occurrence of frost have varied over time. Since the 1950s temperatures have steadily increased, consistent with predictions related to global warming, but follow a nett cooling from the 1910s to the 1950s. Owing to the variability in temperatures and the nature of the botanical data set, no clear relations between low temperatures and plant composition are evident.*

Question 4: What is the influence of fire in Karoo vegetation?

> ***Answer to Question 4****: Fire kills some plant species, some of which are often locally dominant, while most plant species resprout after being burnt. Post-fire shrub growth is slow while grass growth is relatively fast, meaning that structurally fire shifts dwarf shrub/grass communities into temporary sparse arid grassland. Grazing following a fire slows recovery and prevents palatable perennial shrubs and grasses from growing.*

9.2 General Discussion

The Karoo is a semi-arid environment that has been in in a state of climatic flux at evolutionary timescales, and there is firm evidence of climatic fluctuations over the past several millennia (Ecker *et al.*, 2018), and exact measurements of some variables over the past century. Historically, rainfall would have been the most important determinant of botanical composition, though influenced by various climatic factors as well as by defoliation by animals, principally insects and large mammals (Mucina, Rutherford, *et al.*, 2006). With the advent of European colonisation and the influx of fences and windmills, the Karoo over the past approximately 150 years has experienced levels of grazing orders of magnitude higher (sheep alone at least a 10-fold increase (van den Berg *et al.*, 2019)) than before (Archer, 2000), and it is within this context that the Karoo is viewed in this thesis.

At Grootfontein, the first three-quarters of the twentieth century was generally dry, with some severe droughts (Chapter 2). This dry period ended in the mid-1970s when good rains fell and, despite some short droughts, higher rainfall conditions have persisted to present-day.

Concomitant with higher rainfall was an increase in grassiness and a reduction in the density of shrubs (Chapter 3) (Appendix A 1). The increase in grassiness was not of the form experienced earlier in the century, when good rains gave rise to annual and short-lived perennial species such as *Aristida congesta* and *Eragrostis lehmanniana* (O'Connor and Roux, 1995) (Appendix A 2). Rather, the shift was to a grassland-like structure with long-lived, large, tufted grasses such as *Digitaria eriantha*, *Sporobolus fimbriatus*, *Heteropogon contortus*, and *Themeda triandra* being abundant. In some areas, *T. triandra* has created near-monospecific stands that appear structurally and compositionally similar to semi-arid grassland such as the Xhariep Karroid Grassland (Mucina, Hoare, Lötter, *et al.*, 2006) (Appendix A 3). Ongoing monitoring of these patches, and composition generally, will provide insight into the patterns of transition from Nama-Karoo to Grassland that are anticipated to continue should rainfall remain high.

Rainfall variability across the globe is predicted to increase in the face of climate change (Browning *et al.*, 2017), but examples of directional increases in precipitation in recent times in semi-arid areas, such as those described in this thesis, were not found. While rainfall has fluctuated considerably in the past, i.e. series of directional changes, at shorter scales, have certainly occurred (Nicholson, 1989). The novelty of the findings in this work is that that it documents a recent directional increase in rainfall in a semi-arid area for a period long enough to allow botanical composition to change to the extent that there is evidence for a biome-shift. Importantly, botanical composition was indeed measured, and thus provides empirical evidence of the change. The research reported here pertains to the Nama-Karoo and Grassland Biomes, but has relevance in a wider, even global, context owing to the general way in which plants with particular traits respond to rainfall (Ogle and Reynolds, 2004). Additionally, these findings have relevance in ecotonal regions where increasing atmospheric CO_2 concentrations, acting in a manner akin to increased rainfall owing to stomatal closure (Morgan *et al.*, 2011), may allow C_4 grasses to gain hold in a hitherto too-dry environment.

In contrast, should rainfall return to the about-350 mm mark, what will happen? Presumably grasses will die out (Appendix A 4), cover will decrease, and bare patches hitherto occupied by grasses will be colonised by annuals and short-lived species in the short term and shrubs in the long term, as presumably happened, and has been extensively reported on, during the first half of the twentieth century. Unfortunately, the long-term data from Grootfontein give little insight into details of how this might occur because similar conditions have arguably only been recorded once (in about 1900), and no form of vegetation monitoring was yet in effect.

Another aspect of rainfall amount is its seasonality. Seasonality fluctuated markedly over the century, particularly since the 1970s (Chapter 2). However, owing to the nature of the botanical records and the high variability in inter-annual seasonal rainfall (Appendix A 5), it is difficult to extract empirical evidence for the hypothesis that late summer or autumn rains necessarily favour the shrub component, although the evidence seems strong that midsummer rains do strongly favour grass growth.

The nett increase in rainfall from the 1970s to present day appears largely to have surpassed the effects of grazing (Chapter 3). Independent of whether veld was grazed in a lenient or severe way, grasses increased in abundance. Furthermore, this occurred in severely grazed veld both if treatments had been discontinued and if they were maintained. (A caveat here is that because stocking rates were maintained at a constant level as rainfall, and grass, increased, the mass of livestock per mass of vegetation (fodder) decreased, thereby reducing the stocking pressure.) This finding underscores the importance of rainfall as a driver in terms of the general finding that the Karoo has become grassier over the past several decades. Had improvements in veld management, such as better grazing systems and lower stocking rates, been the reason, then it would be expected that veld under treatments of continued severe grazing would have remained in its degraded state.

A key driver of plant growth, and hence livestock productivity, at short and long scales is rainfall variability, where the issue accorded most importance is the occurrence of droughts. Despite several relatively short droughts occurring, the general increase in rainfall experienced in the region since the mid-1970s has meant that forage production (notably grass) has been maintained at a higher level than earlier in the century. Increased grassiness allowed for changes in agricultural practices, notably the expansion of the number of cattle in the Karoo (Potts *et al.*, 2015), as well as ecological disturbances such as fire (Chapter 8). The opportunity to increase the proportion of cattle on a farm may be met with enthusiasm by farmers. First, cattle are less selective feeders than are sheep, which is of benefit to plants and to rangeland health. Second, cattle are less prone to attack by predators, a major problem in the Karoo, and to theft, another ongoing challenge. However, there are also downsides to incorporating cattle into commercial farming enterprises: sheep are generally more profitable than cattle, partly because sheep are often farmed for both meat and wool, and the infrastructure (including fencing) on sheep farms is often not suitable for containing and managing cattle.

Increased rainfall may have (temporarily?) largely removed the nature of the effects that high variability in rainfall usually elicit. Notable examples would include a reduction in the prolonged periods of fodder scarcity, and probably a reduction in the types of droughts that induce the mass mortality of grasses and possibly shrubs (Chapter 4, Chapter 5), as well as the degree to which livestock can degrade veld by inducing shifts in botanical composition (Chapter 3). This new-found stability rests, of course, on livestock numbers being kept at levels recommended before rainfall increased. This has been the case at Grootfontein, where stocking rates prescribed by the state have been adhered to, but may not be the case in farming areas, where stocking rates are usually higher (Danckwerts and Daines, 1981) and farmers may seek to exploit the opportunity afforded by increases in forage availability. This proposition adds support to the general recommendation that it is beneficial to maintain stocking rates at conservative levels (such as those officially recommended in South Africa) rather than trying to have livestock consume all available forage.

The idea that the boundary of the Karoo shifts according to rainfall is well founded. Quite what defines grassland *versus* Nama-Karoo, however, has not been defined, and the implication here is that if there is uncertainty of what constitutes a biome, then defining a biome boundary is not possible. Perhaps this is not important, certainly ecologically and agriculturally. However, in terms of the legal policies that control much of what happens in ecological systems, the distinction might well be of importance. Dealing with the boundary between Nama-Karoo and Grassland Biomes in this thesis, veld was classified as being grassland if it was essentially devoid of Karroid shrubs, and this definition emerged from the general descriptions of the biomes in the literature. However, there are problems with this, because there are areas that are defined as grassland that do indeed have a Karroid component (Mucina, Hoare, Lötter, *et al.*, 2006). Examples in the Grassland Biome include the Xhariep Karroid Grassland, the Bloemfontein Dry Grassland, and the Bedford Dry Grassland. Hence, a clearer conceptual understanding (and definition) of what constitutes the respective biomes is needed. Botanical composition at any point in time is probably too simplistic because 1) individual plant relics may be able to persist for a long time, 2) variation in rainfall (rather than sustained directional shifts) can significantly alter composition (Chapter 5), and 3) episodic disturbances such as fire (Chapter 7, Chapter 8) and drought (Chapter 4) may extirpate species in the short term which re-colonise in the long-term (Appendix A 6). A definition that accommodates the population biology and phenology (notably seed production and recruitment) of key species (or life form) may be necessary. Implicit in this would be the recognition of alternate stable states that persist and may be self-reinforcing, as have been recognised elsewhere (Parr *et al.*, 2012). Without a clearer understanding of what constitutes Grassland and Nama-Karoo Biomes, pronouncements on biome shifts and the position of biome boundaries will remain vague.

Biome shifts have been documented the world over across numerous vegetation types. Numerous causal factors have been invoked, prevalent among which are drought (Martinez-Vilalta and Llorte, 2016), herbivory (Zimov *et al.*, 1995), atmospheric CO_2 concentrations (Bond *et al.*, 2002), and fire (Trollope *et al.*, 2002). In and adjacent to the Nama-Karoo, empirical examples of biome shifts are essentially non-existent (Potts *et al.*, 2015), despite the recognition that historical changes in temperature and rainfall regimes did elicit shifts between Nama-Karoo and Grassland states. The results presented in this thesis present empirical evidence of a biome shift from Nama-Karoo to Grassland Biome, subject to the caveat that there is no precise definition of exactly what constitutes a biome shift.

The notion that the boundaries of the Karoo are changing has a long history. Shaw (1873) noted how overgrazing had led to the expansion of the biome (or at least the expansion in range of various Karroid species), and Acocks (1953) predicted that the Karoo was expanding owing to poor agricultural management practices. More recently, the predictions remain essentially the same, though the causal factors have been replaced. The idea of an expanding Karoo owing to overgrazing has largely been refuted (Hoffman and Cowling, 1990), and been replaced with predictions of an expanding Karoo as a response to climate change. Mechanisms here include increased temperatures and decreased rainfall that will drive expansion of the Karoo into the adjacent Grassland Biome (Ellery *et al.*, 1991; Midgley *et al.*, 2008), and there is ecophysiological evidence that the growth of some Karroid species is enhanced by increases in temperature (Edwardes, 2018). However, the Nama-Karoo Biome is also at risk as it is predicted that the Savanna and Desert Biomes may encroach into it (DEA (Department of Environmental Affairs), 2012).

The evidence from in this thesis finds the opposite occurring (Chapter 3), where grassiness has increased, and it is argued that this is in response to increased rainfall (Chapter 2), consistent with the meteorological predictions of Engelbrecht *et al.* (2009). Tentatively, therefore, this work contributes to the general theme that the Karoo may be encroached upon on several fronts by adjacent biomes.

During times of approximately-constant rainfall, grazing itself exerts a strong influence over plant composition. Foremost in importance appears to be season of grazing or, more specifically, the influence of repeated summer grazing on botanical composition. Under such a system, grasses decline in abundance and shrubs increase (Chapter 4) (Appendix A 7). This supports the hypothesis that grasses grow best when it is hot and moisture is available. Grazing during this time prevents grasses from accumulating leaf material and, hence, root reserves, and they die out. Exceptions are those species, such as *Tragus koelerioides*, that can escape from grazing by remaining short and out of the reach of livestock, and hard grasses of lower palatability such as *Aristida diffusa* (Appendix A 8). While this finding is ecologically useful, it has less direct relevance in the agricultural community. Historically it is unlikely that there were many farms where individual paddocks were grazed repeatedly in summer. (In contrast, it is commonplace that certain paddocks are overgrazed in a general sense in the long-term, especially those paddocks that are close to a farmhouse or handling facilities. Such paddocks are often termed *huiskampe* (home-paddocks) and are often degraded. This was noted when the Camp 6 and subsequent grazing trials were designed – it was recognised that such treatments were not reflective of actual grazing systems, but rather provided insight into plant/animal interactions. There is definite utility in the findings, though. First, it provides possible guidance on how to manage for increased grassiness – for example, resting paddocks in summer will likely increase grassiness, as will resting grasses in general in summer following a drought. An important future research problem would be to understand the influence of soils and geology on the ability of grasses to survive summer grazing, and which veld types are most tolerant of grazing once a drought has been broken. Second, it offers farmers managerial freedom of movement: because grasses generally persisted under heavy midsummer grazing, provided that this was not repeated year after year, this implies that occasional severe summer grazing should not lead to a loss of grasses from a system.

The response of grasses to summer grazing can be fairly reliably predicted based on growth form (mainly height) and palatability to animals. For shrubs, a separate set of rules may apply. Shrubs in general increase under conditions of summer grazing, possibly because of reduced competition from grasses (Chapter 4). Beyond that, there is a dearth of information that would be needed to construct predictive models on how species might respond to treatments such as summer grazing. Notably lacking is an understanding of the growth of individual plants in relation to weather, resource availability, and herbivory that would require research on shrub phenology and morphology, including *inter alia* drought-induced deciduousness, chemical and physical anti-herbivore defences, root carbohydrate storage, absorption of water from dew, carbohydrate relocation during flowering, and growth from dormant buds. These are all intriguing research questions for the future, and should be examined to develop an understanding of shrub mortality, survival, and regeneration.

A question that emerged during this study, and pervades many interpretations and conclusions, though is only indirectly reported on, is how plants should be grouped according to functional type. In this thesis, plants were examined according to species and according to growth form. This offers a fairly robust approach to interpreting ecological shifts, but would benefit from refinement into biologically more meaningful groupings. On a species level, some species may be floristically distinct but functionally could probably be combined. These include various species within the shrub genera *Delosperma*, *Lycium*, *Stachys*, *Chrysocoma*, and *Wahlenbergia* owing to the physical similarity of some species. For the grass species, the opposite is sometimes true – there are distinct growth forms within, for example, the species *Digitaria eriantha* and *Eragrostis curvula*. Growth forms would also benefit from some attention. Currently grasses have been separated according to longevity – perennial *versus* annual – but some species seemingly straddle both groups. *Eragrostis lehmanniana*, for example, acts as a perennial grass in that it can persist for many years. It also acts similarly to annual grasses in that it germinates immediately and *en masse* following rain, and it will die following a short drought. There are more examples on this theme, but an in-depth discussion falls outside the scope of this thesis. However, as our understanding of Karoo ecology increases, interpretation of botanical dynamics would benefit from refinement of how functional types are defined.

The responses of plant cover to increased rainfall is evident in the results from the Boesmanskop site (Chapter 5). As expected, bare ground decreased with increasing rainfall, and shrubs performed unexpectedly well, showing a significant increase in cover over time.

This would refute a hypothesis that good rains would favour grass growth at the expense of shrub growth, i.e. that shrubs would be at a competitive disadvantage under such conditions. Here again our lack of understanding about shrub growth is evident, and insufficient to construct a meaningful prediction. Obvious reasons might include the underground storage of shrubs, seasonality of rainfall, which is tied to growing season, and the effects of short droughts on grasses *versus* shrubs.

The length of the growth season in this thesis was defined as the period from the last frost to the first frost of the following season (Chapter 6). This was used owing to the resolution at which responses were being investigated and the nature of the data sets at hand. However, a driver of potential importance is the period of growth from the first rains to the first frost – i.e. the growth season for grasses (Wiegand *et al.*, 2004). The Boesmanskop data, coupled with information of temperatures and rainfall, would allow this question to be examined, at least at a coarse level. Again, focused information at plants and small plot levels on growth of plants in response to rainfall at different times of year are needed. Despite being an ecological driver of obvious importance, information on minimum temperatures and frost, at the resolution investigated in this thesis, yielded relatively little insight into temperature/vegetation correlations. It did, however, highlight the level of variation that occurs in the eastern Karoo, and that minimum temperatures fluctuate at large temporal scales.

Plant cover and survival (and hence mortality) have typically been interpreted in the context of seasonal rainfall, and sometimes sub- or multi-season rainfall, and this has provided much insight into these issues. However, it is clear that the mortality of plants, particularly shrubs, cannot be predicted by rainfall alone (Chapter 4). The extensive mortality of shrubs in the early 1950s at Grootfontein is a good example of this. Rainfall is of obvious importance here because it is the primary supply of water. But other variables affect water availability: two that are immediately apparent are temperature and relative humidity. These in combination influence firstly dew-point, and dew in arid environments can be a very important supply of water, and secondly evapotranspiration. High humidity coupled with frequent dew would provide a very different survival environment to plants from low humidity and no dew, even across the same temperature regimes. This remains unexplored but may provide important insight into Karoo plant growth dynamics.

The immediate response of grass to rainfall, both in germination of new plants and increase in biomass of existing plants, is well documented (Cowling and Roux, 1987; Hoffman, 1989; Milton *et al.*, 1990; van Rooyen, 2004). The response is so dramatic that, under conditions of high rainfall, fine fuel biomass can increase far faster than it can be consumed by livestock (Booysen and Tainton, 1984). Owing to the climate of the Karoo, this grass biomass cures and is swiftly rendered combustible. Given weather conditions that are conducive to fire-spread (high enough wind speeds and temperatures, and low enough relative humidity), and a source of ignition, ensuing fires can spread quickly and consume large areas. Such fires are relatively rare, being constrained by the low incidence of ignitions, the generally low rainfall of the Karoo, and the ongoing removal of biomass by livestock.

The work here shows that the effect of Karoo fires on vegetation depends on growth form and post-fire grazing (Chapter 7, Chapter 8). In general, grasses recover quickly, re-sprouters stay alive but regrow slowly, and non-sprouters are extirpated, re-colonising probably several years to several decades after a fire. If veld is rested, then recovery (or return to the initial condition) is faster than if veld is grazed, and the heavier the grazing the slower the recovery. Despite interesting revelations, much remains unanswered. The resprouter/non-sprouter status of most Karoo shrub species is unknown; the influence of the severity of grazing on post-fire plant growth is unknown; the patterns of colonisation of non-sprouters is unknown. Add to this the variation in rainfall and the possibility of second burns, and it can be concluded that current insight into fire effects on Karroid vegetation is nearly non-existent. Fortunately, however, the ongoing study opportunities afforded by occasional wildfires, the relative ease by which botanical communities can be described, and the vast array of information provided on fires through satellite imagery means that our understanding of this phenomenon can be addressed to a useful extent with relative ease.

As in other systems with both slow-growing woody and fast-growing grassy components, the persistence and biomass of grasses may be strengthened by a positive-feedback grass/fire loop (Accatino *et al.*, 2010). Examples of such feedbacks with the grass *Eragrostis lehmanniana*, the same species that often dominates in the eastern Karoo, are found in North America, where the species is invasive (Villarreal *et al.*, 2016). A fire/grass feedback loop would be expected in the Karoo if rainfall remains high, but might also be able to persist under normal rainfall conditions if fire induces a replacement of woody shrubs with grasses (i.e. grasses increase in abundance) and the return-time of fire is sufficient to keep woody biomass low. This would be an example of where either of two alternate states could persist given the occurrence of occasional fires. It is useful to note here that despite occasional wet years giving rise to landscapes with a high fuel load, fires continue to be rare occurrences. This is because, as with many other areas, sources of ignition (e.g. sparks, lightning) are rare. It follows that occurrences of fire-maintained Karroid grasslands would presumably be higher in areas where ignition events are more frequent, such as near towns, dwellings, and roads.

The research presented in Chapter 7 and Chapter 8 clearly demonstrates that fire can convert, at least structurally if not botanically, Karroid shrublands into sparse grassland. Furthermore, it demonstrates that 'recovery' is not merely a process of regrowth, as is the case with many savanna systems, but also of re-colonisation, often by species that were dominant pre-fire. Additionally, it demonstrates that post-fire grazing influences recovery, particularly of dwarf shrubs. This can be an important issue in the Karoo, where post-fire livestock management may play an important role in recovery following fire.

If a positive feedback grass/fire loop emerges in the Karoo, it may necessitate a shift in agricultural practices in affected areas. First, the proportion of cattle will likely have to be increased to be able to usefully exploit the more abundant, though lower-quality, grass that will presumably come to dominate. Second, farmers will have to adapt to farming in a fire-prone environment, which would necessitate improved fire-management on farms (including the establishment of a firebreak burning programme) and a shift to fire-adapted infrastructure (such as fences with metal droppers and standards). Modifications to grazing systems and fodder-reserve plans might similarly need attention. Such changes will require financial investment and a change in the managerial approach to farming. However, the intended outcomes of such endeavours are well defined, even now, because in essence these are the current agricultural norms of the grassy regions to the north and the east of the Nama-Karoo Biome.

9.3 Towards an improved model of vegetation dynamics in the eastern Karoo

Milton and Hoffman (1994) produced a hallmark paper that presents a state-and-transition model of eastern Karoo vegetation dynamics as influenced by grazing and rainfall. Here, findings from the research presented in this thesis are used to revisit their findings in order to find support for, and contradictions to, the model, and provide suggestions for how it may be refined in the future. The discussion below follows the states and their transitions as illustrated in Figure 4 of that paper. For brevity, State 1, State 2 … are presented as S1, S2 … and Transition 1, Transition 2 … are presented as T1, T2 …. In each case, a summary of two states and their transitions are summarised, and then discussed in light of the findings presented in this thesis. (States and transitions as described in the Milton and Hoffman (1994) paper are accepted as 'correct', but potential modifications are noted.)

Summary: S1 ↔ S2

S1 represents veld in 'good' condition, which is a co-dominance of shrubs and perennial and short-lived grasses (species are given). S2 represents veld in 'better' condition, where perennial grasses have recruited at the expense of short-lived grasses. Under conditions of consecutive years of above-average summer rains (T1), perennial grasses recruit, vegetation becomes more grassy, and the incidence of short-lived species decreases.

Discussion: S1 ↔ S2

S1 would benefit from the inclusion of nonsprouting species such as *Eriocephalus ericoides* and *Ruschia intricata*, because they are often locally dominant (Chapter 8) and also are killed by fire (Chapter 2, Chapter 8; see below). Alternatively, S1 could be split into two variants, one where non-sprouters are dominant, and one where resprouters are dominant. In S2, it appears that short-lived species continue to thrive even under conditions of many years of high rainfall (Chapter 3), presumably because not all physical gaps are occupied. An exception may be when dense stands of *Themeda triandra* develop (Chapter 3), which in essence indicates a transition from Nama-Karoo to Grassland Biome. The competitive influence of grasses will likely decrease shrub populations rather than allowing them to remain approximately constant (Chapter 3). Therefore, S2 should include short-lived species, and a further state might be introduced depicting a grassland state, which would also imply an exit from the model in that it no longer relates to Nama-Karoo.

Summary: S1 ↔ S3

S1 as above. S3 represents veld in 'degraded' condition in response to summer droughts and summer grazing. Perennial grasses have largely been extirpated owing to these disturbances.

Discussion: S1 ↔ S3

‘Summer grazing’ needs to be clarified. It appears that summer grazing is fully compatible with healthy Karoo veld as long as not all grazing occurs in summer (i.e. approximately fourfold higher stocking densities in order to maintain a constant long-term stocking rate), and this grazing does not occur over consecutive summers in the long term (Chapter 4). Implicit in this statement is that heavy summer stocking is acceptable if subsequent summer rests occur, and continuous grazing is acceptable because stocking density is not unduly high in summer. However, it appears that despite continuous grazing being preferable to repeated heavy summer grazing, other systems (forms of rotational grazing) are superior.

Perennial grasses are not extirpated as a whole under even severe grazing treatments (Chapter 4). Rather, perennial grasses can survive, though probably at lower densities, if they have a prostrate growth habit (e.g. *Tragus koelerioides*) or if they are relatively unpalatable (e.g. *Aristida diffusa*).

Summary: S1 ↔ S4

S1 as above. S4 is a further degraded state owing to long-term continuous selective grazing.

Discussion: S1 ↔ S4

This component was not addressed directly, but the notion of long-term continuous grazing leading to a degraded shrubland was not evident. This may be because stocking rates at the Grootfontein trials were kept at recommended levels. Analysis of data emanating from other treatments, where stocking rates were high, would help to clarify this issue. The importance of *Tragus koelerioides* and similar grasses may have been overlooked (Chapter 4).

Summary: S4 ↔ S5

S4 as above. S5 is a highly degraded, denuded state, initiated by long-term heavy continuous overgrazing. Active intervention is needed to allow revegetation.

Discussion: S4 ↔ S5

This component was not addressed directly. However, evidence of post-fire recovery on town commonages, which are heavily and continuously grazed (Chapter 8), suggests that Karoo vegetation may be more resilient than predicted. The summer-only grazed treatments, with grazing occurring during some drought periods (Chapter 4) were the most severely degraded sites at Grootfontein, and an increase in rainfall was sufficient, even in the treatments were continued, to allow considerable recovery. Accordingly, S5 might be removed from the model, or alternatively noted that this state occurs perhaps only under certain conditions, such as on highly erodible soils.

Summary: S5 → S6

S5 as above. S6 is degraded veld that has been revegetated with pastures or drought fodder crops.

Discussion: S5 → S6

This component was not addressed in the thesis.

New States and Transitions

The model may benefit from the inclusion of additional states and transitions. S7 would be a semi-arid grassland developing if veld is burnt. This state could emerge from S1, S2 and S3 (possibly S4) given the appropriate transitional conditions which include rain-induced increases in fuel load (grass), and ignition. Return from S7 to the original states would be fastest in the absence of grazing, and slowest (or even non-existent) in the presence of heavy grazing. Resprouting species would recover relatively quickly, while nonsprouting species would take somewhere between 10 and 40 years to recover (Chapter 7). If a grass/fire feedback loop developed, then S7 would be persistent.

S8 would be veld dominated by large, tufted, perennial grass species, with a relic Karroid component. Whether this would constitute Grassland or Nama-Karoo remains undefined. This state would emerge from S2, and come about after many years of above-average annual rainfall, returning to its original state if rainfall conditions returned to average.

9.4 What have we learned?

The monthly rainfall data from Grootfontein is a valuable record and its analysis provided some important new insights (Chapter 2). Two of these are key. First, much of the first half of the twentieth century was plagued by severe droughts. These coincided with the dramatic increase of livestock numbers in the area, and also with the inception of scientific examination of Karoo veld and its response to herbivory from livestock. Thus the well-reported deterioration of the condition of Karoo veld is confounded with the occurrence of severe droughts, and the relative impact of herbivory *versus* drought remains unclear. Second, the eastern Karoo has experienced what may be described as an increased shift in rainfall since approximately the mid-1970s. The main effect of this has been to greatly increase the grassiness of the area, to the point where some areas have arguably shifted to grassland, although the persistence of this state remains to be seen (Chapter 3). This fits in with our understanding that areas near the current-day boundary of the Karoo have oscillated between shrubland and grassland states for long periods of time. It also demonstrates that rainfall must be carefully examined when interpreting vegetation dynamics in other parts of the Karoo, where nett increases in grassiness have also been shown (Appendix A 9).

Chapter 4 confirms and provides additional insight into the damaging effects of summer grazing on botanical composition but also provides, perhaps more importantly, a caveat that summer grazing is severely damaging only when it is repeated year after year (less than ten years at the Seligman site), and when stocking densities are high (i.e. summer stocking rates are increased four-fold, but occur during only a quarter of the year). Accordingly, summer grazing when occurring during continuous grazing (repeated summer grazing but at lower stocking densities) and rotational grazing (heavy summer grazing followed by complete summer rests) do not induce catastrophic collapses in condition of veld. Importantly, the incidence of heavy summer-only grazing on farms in the Karoo is likely rare to the point on being non-existent, and grazing of such a severity (though not summer-only) probably only takes place in the commonages around some towns, where animal numbers can be very high. The chapter also highlights our lack of understanding of the ecology of dwarf shrubs in response to both grazing and rainfall. In contrast, our models of grass growth are more robust, as exemplified in Chapter 5.

The examination of low temperatures (Chapter 6) revealed three findings of potential general importance in understanding Karoo ecology. First, temperatures are often far lower than is generally reported, with potentially important implications for understanding plant physiology in the area. Second, the length and ‘coldness’ of the non-growing season does indeed fluctuate considerably, and may reasonably be expected to influence botanical growth and composition that might be assessed with appropriate experiments. Third, minimum temperatures became lower from the early- to the mid-20th century, and subsequently increased. This pattern should be considered when interpreting trends in temperature or other variables in the context of global warming.

The examination of fire in the Karoo, using a detailed single-site study (Chapter 7) and a low-resolution regional observational study (Chapter 8) yielded the foundations of the first conceptual model of the influence of fire in the Nama-Karoo. It was found that some dwarf shrubs survive fire and re-sprout, while others (often locally dominant) are killed and recolonise through seed. The recovery process or, rather, the return to the pre-fire condition, is relatively slow, in particular for shrubs, and appears to be influenced by herbivory, especially at high stocking rates. Depending on the degree to which grasses replace shrubs, and the incidence of future fires, it is proposed that a fire/grass feedback loop might be initiated that would shift Karroid vegetation to a type of sparse arid grassland.

9.5 What are implications for Karoo management?

Global predictions of climate change point universally to a future world where climate variability is higher than is presently the case, and an atmosphere that allows faster growth of C_3 species, and in some cases C_4 species. Local predictions for the eastern Karoo are varied, with some suggestion of increased long-term rainfall that has, thus far, been supported by rainfall records. In combination, this may point to a wetter eastern Karoo that is grassier, but will be punctuated by severe weather extremes, notably drought. Owing to the increased grassiness, fire is likely to become a disturbance of increasing incidence and, given its potential effects, much increased importance.

What are the implications to farmers and other land-users? First is that if high rainfall conditions persist, then the carrying capacity of the region will increase. This should allow more animals to be stocked, but similarly it must be recognised that increased climatic variability might play out in the form of occasional intense droughts, in which case a prudent approach would be to retain livestock levels at conservative stocking rates or, failing that, to be able to sell off livestock if necessary. Second, increased grassiness may increase the suitability of the area for cattle production. Third, and linked to the second point, is that high-rainfall seasons would provide the opportunity to speculate in livestock (mainly cattle), probably by buying young animals to grow and hopefully fatten over the short term (perhaps six months to a year). Fourth, an increased incidence of fire has the potential to destroy food reserves in the short term, and to cause severe damage to livestock, fencing, equipment, and to endanger human life. Interventions to mitigate such effects should include training to better understand fire behaviour and control, the development of fire associations for legal and control reasons, and consideration of interventions to increase the chance of successful fire control, including firebreaks, investment in fire-fighting equipment, and even landscape-level grazing management designed to increase the discontinuity of fuel-loads, thereby reducing the ability of fire to spread.

9.6 Where to from here?

To finish are some thoughts on the direction of future research activities that would help to address gaps in our knowledge that the work presented here has highlighted.

To begin, it is recognised that much of the information that has been reported on emerged from long-term grazing trials. These trials were initiated with purely agricultural goals in mind, but their utility far exceeds these in terms of their contribution to Karoo ecology in a more general sense. Many similar trials in other areas have been terminated or have merely lapsed, and special effort should be made that this does not happen to the Grootfontein trials. As of the beginning of 2019, the Camp 6, Bergkamp (not reported on here) and Boesmanskop trials are all still in existence as registered research projects, but the Camp 6 trials have been destocked for several years, the Bergkamp trials for two years, and sheep were absent from the Boesmanskop research trials for about a year (this was remedied). Judging by the mortality rate of other long-term trials, a new approach, perhaps involving other stakeholders, may be needed to ensure the survival of these ecological gems.

The major themes in this thesis were rainfall, grazing and fire. Fire is something of a novelty in the Karoo, though is perhaps becoming more important. Such studies in this environment must probably necessarily be done opportunistically by studying accidental fires rather than establishing experiments. At Grootfontein, the study of Karoo fires is an active research project, and is receiving attention from other institutions as well. Two key aspects that should be addressed are identified. First is the recovery of re-sprouters and the establishment of non-sprouters over time, and the modifying influences of grazing, in particular, as well as rainfall. Second is the development of a conceptual model for post-fire management of Karoo veld. The notion of resting the veld long enough for botanical composition to return to its pre-burn state is unreasonable owing to the long time periods required, and a “best-management” approach for say a decade post-fire should be identified. This is also important for when farmers need to estimate the quantum of damages incurred if their land is burnt.

In terms of grazing, it may be argued that the range of responses to herbivory treatments that have been empirically observed fall well short of the types of ‘desertification’ or ‘collapse’ that have been predicted from time to time. As such, this is an indication of how resilient veld in the eastern Karoo appears to be. Even under extreme disturbance regimes of various combinations of drought, severe grazing, and fire, there was no evidence of an irreversible system crash. Thus, the research into grazing systems and stocking rates that was conducted in past decades was presumably successful.

However, there certainly are examples of heavily degraded landscapes in the Karoo, and these must have been caused by something. The causal factors require investigation. Edaphic factors are likely of key importance, and in general this component is often lacking in ecological research efforts in the Karoo. Another avenue for further research is the interaction between plant survival (notably seedlings), rainfall, and grazing. Should grazing prove to be a potent determinant of plant survival at key times, such in the aftermath of drought, then appropriate research may yield managerial options for interventions that may have important implications for both ecological health and agricultural productivity. It is envisaged that some small plot-based experiments, perhaps in conjunction with water-limiting structures, would provide key insight into this aspect of Karoo ecosystem functioning.

Perhaps the largest gap in our understanding of Karoo ecology is the biology of dwarf shrubs, and their response to grazing and, more importantly, rainfall (both drought and high water availability). It is suggested that individual-plant based approaches, rather than the hitherto more common approach of measures of abundance, should be followed. Small manipulative experiments, including adjusting grass/shrub ratios, defoliation (through grazing or clipping), and moisture-limitation (through rain shelters) would provide a solid basis from which to start. Additionally, monitoring established and new (seedling) populations of dwarf shrubs across various environmental and grazing gradients is needed.

A theme in the work presented here has been the high levels of intrinsic variability in many natural ecosystem drivers. In the future, global climate change adds another layer of complexity. It is possible that the types of responses presented here and elsewhere will be exacerbated in a warming world. For the Karoo, several issues require investigation in this context. First is a more detailed examination of climatic variability and change, and how these may affect ecosystems. Second, the increasing grassiness of the Karoo needs to be studied in much greater detail, because grass influences many ecological and agricultural aspects, including fodder availability and hence carrying capacity, occurrence of fire, cover and hence water retention and availability in soils, and the competitive influence on, and thus prevalence of, shrubs.

REFERENCES

***Note**: The referencing style in the body and in this section follows that of the journal "Evolutionary Ecology Research"*

Abatzoglou, J.T. and Kolden, C.A. 2011. Climate change in western US deserts: potential for increased wildfire and invasive annual grasses. *Rangel. Ecol. Manag.*, **64**: 471–478.

Accatino, F., De Michele, C., Vezzoli, R., Donzelli, D. and Scholes, R.J. 2010. Tree-grass co-existence in savanna: interactions of rain and fire. *J. Theor. Biol.*, **267**: 235–242.

Acocks, J.P.H. 1953. *Veld types of South Africa.* Pretoria: Government Printer.

Addinsoft. 2013. Data Analysis and Statistics with Microsoft Excel. Paris: Addinsoft.

Adler, E.D. 1953. Planning Against Drought. *Farming in South Africa*, **23**: 41–42, 46.

Alexander, L. V., Zhang, X., Peterson, T.C., Caesar, J., Gleason, B., Klein Tank, A.M.G., *et al.* 2006. Global observed changes in daily climate extremes of temperature and precipitation. *J. Geophys. Res. Atmos.*, **111**: 1–22.

Alexander, W.J.R., Bailey, F., Bredenkamp, D.B., van der Merwe, A. and Willemse, N. 2007. Linkages between solar activity , climate predictability and water resource development. *J. South African Inst. Civ. Eng.*, **49**: 32–44.

Altatoron. 2007. The Nama Karoo ecoregion. File:AT1314 map.png.

An, S.-I. and Wang, B. 2000. Interdecadal change of the structure of the ENSO mode and its impact on the ENSO frequency. *J. Clim.*, **13**: 2044–2055.

Anderson, P.M.L. and 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. *J. Arid Environ.*, **70**: 686–700.

Andrew, J. 1889. Notes on Angora goat farming. *Pap. Proc. R. Soc. Tasmania*, **1**: 31–38.

Andrews, C.J. 1996. How do plants survive ice? *Ann. Bot.*, **78**: 529–536. Annals Botany Co.

Anon. 1983. *Drought Management Practices*. Department of Agriculture: Karoo Region Middelburg.

Archer, E.R.M. 2004. Beyond the '" climate versus grazing "' impasse : using remote sensing to investigate the effects of grazing system choice on vegetation cover in the eastern Karoo. *J. Arid Environ.*, **57**: 381–408.

Archer, S. 2000. Technology and ecology in the Karoo: a century of windmills, wire and changing farming practice. *J. South. Afr. Stud.*, **26**: 675–696.

Arnalds, O. and Archer, S. 2000. *Rangeland Desertification* (O. Arnalds and S. Archer, eds). Dordrecht, The Netherlands: Springer Science + Business Media.

Bath, D.F. 1975. Diseases caused by organic poisons: urea, acidosis, phosphate. *Wool Prod. Leafl. E 6.4 / 1975*, 1–4.

Bedford, B. and Roberts, B.R. 1975. Commercial sheep production from continuous and rotational grazing over thirty-five years in the Karoo. *Proc. Annu. Congr. Grassl. Soc. South. Africa*, **10**: 123–131.

Belsky, A.J. 1990. Tree / grass ratios in East African savannas : a comparison of existing models. *J. Biogeogr.*, **17**: 483–489.

Beukes, P.C. and Cowling, R.M. 2003. Non-selective grazing impacts on soil-properties of the Nama Karoo. *J. Range Manag.*, **56**: 547–552.

Bond, W., Woodward, F.I. and Midgley, G.F. 2002. Does elevated CO_2 play a role in bush encroachment. In: *Multiple Use Management of Natural Forests and Savanna Woodlands: Policy Refinements and Scientific Progress. Proceedings of Natural Forests and Savanna Woodlands Symposium*, pp. 6–9.

Bond, W.J. 2008. What Limits Trees in C_4 Grasslands and Savannas? *Annu. Rev. Ecol. Evol. Syst.*, **39**: 641–659.

Bond, W.J. and Keeley, J.E. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends Ecol. Evol.*, **20**: 387–394.

Bond, W.J. and Midgley, J.J. 2003. The evolutionary ecology of sprouting in woody plants. *Int. J. Plant Sci.*, **164**: 103–114.

Bond, W.J., Stock, W.D. and Hoffman, M.T. 1994. Has the Karoo spread? A test for desertification using carbon isotopes from soils. *S. Afr. J. Sci.*, **90**: 391–397.

Bond, W.J. and Van Wilgen, B.W. 1996. *Fire and Plants*. London: Chapman & Hall.

Booysen, J. and Rowswell, D.I. 1983. The drought problem in the Karoo areas. *Proc. Annu. Congr. Grassl. Soc. South. Africa*, **18**: 40–45.

Booysen, P. de V. 1984. Preface. In: *Ecological Effects of Fire in South African Ecosystems* (P. de V Booysen and N. M. Tainton, eds), pp. VII–X. Berlin Heidelberg New York Tokyo: Springer-Verlag.

Booysen, P. de V and Tainton, N.M. 1984. *Ecological effects of fire in South African ecosystems*. Springer-Verlag.

Bosman, F.H. 1942. Spineless Cactus. *Farming in South Africa*, **17**: 665–667.

Botha, W. v D., Du Toit, P.C. V, Blom, C.D., Becker, H.R., Olivier, D.J., Meyer, E.M., *et al.* 2001. *Grazing Index Values (GIV) for Karoo Plant Species* (L. van den Berg and M. van Lingen, eds). Grootfontein Agricultural Development Institute.

Brooks, M.L. and Matchett, J.R. 2006. Spatial and temporal patterns of wildfires in the Mojave Desert, 1980-2004. *J. Arid Environ.*, **67**: 148–164.

Brown, J.C. 1875. *Hydrology of South Africa*. London: Henry S King & Co.

Brown, J.C. 1877. *Water supply of South Africa*. Edinburgh; London: Oliver & Boyd; Simpkin, Marshall, & Co.

Browning, D.M., Maynard, J.J., Karl, J.W. and Peters, D.C. 2017. Breaks in MODIS time series portend vegetation change: Verification using long-term data in an arid grassland ecosystem: Verification. *Ecol. Appl.*, **27**: 1677–1693.

Caroprese, M. 2008. Sheep housing and welfare. *Small Rumin. Res.*, **76**: 21–25.

Cheney, P. and Sullivan, A. 2008. *Grassfires: fuel, weather and fire behaviour*. CSIRO Publishing.

Clarke, P.J., Lawes, M.J. and Midgley, J.J. 2010. Resprouting as a key functional trait in woody plants – challenges to developing new organizing principles. *New Phytol.*, **188**: 651–654.

Clarkson, N.M. and Lee, G.R. 1988. Effects of grazing and severe drought on a native pasture in the traprock region of southern Queensland. *Trop. Grasslands*, **22**: 176–183.

Cleveland, W.S. 1979. Robust locally weighted regression and smoothing scatterplots. *J. Am. Stat. Assoc.*, **74**: 829–836.

Collins, S.L., Glenn, S.M. and Gibson, D.J. 1995. Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. *Ecology*, **76**: 486–492.

Cowling, R.M. 1986. *Description of the Karoo Biome project*. National Scientific Programmes Unit: CSIR.

Cowling, R.M. and Roux, P.W. 1987. *The Karoo Biome: a preliminary synthesis. Part 2 - vegetation and history*. CSIR, Pretoria.

Cronje, P.B. 1992. Glucose-Metabolism and Adrenal-Function in Goats Bred for Fiber Production (Angora-Goat) or Meat Production (Boer Goat). *S. Afr. J. Anim. Sci.*, **22**: 149–153.

Crosti, R., Ladd, P.G., Dixon, K.W. and Piotto, B. 2006. Post-fire germination: the effect of smoke on seeds of selected species from the central Mediterranean basin. *For. Ecol. Manage.*, **221**: 306–312.

Cuddington, K. 2011. Legacy effects: the persistent impact of ecological interactions. *Biol. Theory*, **6**: 203–210.

Danckwerts, J.E. 1989. Plant growth and response to defoliation. 3.1 Grass growth and response to defoliation. In: *Veld Management in the Eastern Cape* (J. E. Danckwerts and W. R. Teague, eds), pp. 8–19. Pretoria: Department of Agriculture and Water Supply, Government Printer.

Danckwerts, J.E. and Daines, T. 1981. Animal production off grassveld. *Proc. Grassl. Soc. South. Africa*, **16**: 19–22.

Davies, R.A.G., Botha, P. and Skinner, J.D. 1986. Diet selected by springbok *Antidorcas marsupialis* and merino sheep *Ovis aries* during Karoo drought. *Trans. R. Soc. South Africa*, **46**: 165–176.

Davies, R.A.G. and Skinner, J.D. 1986. Spatial utilisation of an enclosed area of the Karoo by springbok *Antidorcas marsupialis* and Merino sheep *Ovis aries* during a drought. *Trans. R. Soc. South Africa*, **46**: 115–132.

DEA (Department of Environmental Affairs). 2012. *LTAS Phase I: Technical Summary*. Pretoria, South Africa.

Dean, W.R.J., Hoffman, M.T., Meadows, M.E. and Milton, S.J. 1995. Desertification in the semi-arid Karoo, South Africa: review and reassessment. *J. Arid Environ.*, **30**: 247–264.

Desmet, P.G. and Cowling, R.M. 1999. The climate of the karoo – a functional approach. In: *The Karoo: ecological patterns and processes* (W. R. J. Dean and S. Milton, eds), pp. 3–16. Cambridge: Cambridge University Press.

Donaldson, C.H. 1989. Seedling survival and dryland production potential of grasses and shrubs during the establishment period. *Karoo Agric*, **4**: 3–10.

Donaldson, C.H. 1986. The Camp no. 6 veld grazing trial: An important milestone in the development of pasture research at the Grootfontein College of Agriculture. *Karoo Agric*, **3**: 1–6.

Downing, B.H., Robinson, E.R., Trollope, W.S.W. and Morris, J.W. 1978. Influence of macchia eradication techniques on botanical composition of grasses in the Döhne sourveld of the Amatole mountains. *Proc. Annu. Congr. Grassl. Soc. South. Africa*, **13**: 111–115.

Dreber, N., Oldeland, J. and van Rooyen, G.M.W. 2011. Species, functional groups and community structure in seed banks of the arid Nama Karoo: grazing impacts and implications for rangeland restoration. *Agric. Ecosyst. Environ.*, **141**: 399–409.

du Preez, C. 1971. *K-Gf. 109/1 The production potential of Karoo veld: growth and yield of karoobush and reaction to pruning. 1967-1971. Final Report*.

du Toit, H.S.D., Gadd, S.M., Kolbe, G.A., Stead, A. and van Reenen, R.J. 1923. *Final Report of the Drought Investigation Commission*. Cape Town: Cape Times Limited, Government Printers.

du Toit, J.C.O. 2013. [Camp 6 compositional data 1949-2011]. Unpublished data.

du Toit, J.C.O. 2015. [Grootfontein rainfall data 1988 - 2015] Unpublished data.

du Toit, J.C.O. 2010. An analysis of long-term daily rainfall data from Grootfontein, 1916 to 2008. *Grootfontein Agric*, **10**: 24–36.

du Toit, J.C.O. 2014. Description of very wet to very dry periods at Grootfontein, eastern Karoo: 1889-2012. *Grootfontein Agric*, **14**: 42–50.

du Toit, J.C.O. 2017. Droughts and the quasi-20-year rainfall cycle at Grootfontein in the eastern Karoo, South Africa, 1889-2016. *Grootfontein Agric*, **17**: 36–42.

du Toit, J.C.O. and Nengwenani, T.P. 2013. [Boesmanskop compositional data 2007-2013]. Unpublished raw data.

du Toit, J.C.O. and O'Connor, T.G. 2014. Changes in rainfall pattern in the eastern Karoo, South Africa, over the past 123 years. *Water SA*, **40**: 453–460.

du Toit, J.C.O. and O'Connor, T.G. 2016a. Changes in rainfall seasonality (1889-2015) at Grootfontein, South Africa. *Grootfontein Agric*, **16**: 16–20.

du Toit, J.C.O. and O'Connor, T.G. 2016b. Minimum temperatures and frost at Grootfontein in the eastern Karoo, South Africa, over 98 years. *Trans. R. Soc. South Africa*, **72**: 39–46.

du Toit, J.C.O., O'Connor, T.G. and van den Berg, L. 2015. Photographic evidence of fire-induced shifts from dwarf-shrub- to grass-dominated vegetation in Nama-Karoo. *South African J. Bot.*, **101**: 148–152.

du Toit, J.C.O., Ramaswiela, T., Pauw, M.J. and O'Connor, T.G. 2018. Interactions of grazing and rainfall on vegetation at Grootfontein in the eastern Karoo. *African J. Range Forage Sci.*, **35**: 267–276.

du Toit, J.C.O., van den Berg, L. and O'Connor, T.G. 2015. A summary of rainfall at the Carnarvon Experiment Station, 1931-2013. *Grootfontein Agric*, **15**: 27–35.

du Toit, J.C.O., van den Berg, L. and O'Connor, T.G. 2014. Fire effects on vegetation in a grassy dwarf shrubland at a site in the eastern Karoo, South Africa. *African J. Range Forage Sci.*, **32**: 13–20.

du Toit, P.C.V. 1988. Diets selected by Merino and Dorper sheep in Karoo veld. *Karoo Agric*, **2**: 15–22.

du Toit, P.C. V. 2001. A study of animal production under different grazing regimes in the False Upper Karoo at Grootfontein. *African J. Range Forage Sci.*, **18**: 137–141.

du Toit, P.C. V. 2002a. Animal production under different grazing regimes at Grootfontein. *Grootfontein Agric*, **4**: 1–7.

du Toit, P.C. V. 2002b. Boesmanskop grazing-capacity benchmark for the Nama-Karoo. *Grootfontein Agric*, **5**: 1–6.

Duker, R., Cowling, R.M., du Preez, D.R. and Potts, A.J. 2015. Frost , Portulacaria afra Jacq ., and the boundary between the Albany Subtropical Thicket and Nama-Karoo biomes. *South African J. Bot.*, **101**: 112–119.

Duker, R., Cowling, R.M., du Preez, D.R., Vyver, M.L., Weatherall-Thomas, C.R. and Potts, A.J. 2015. Community-level assessment of freezing tolerance: frost dictates the biome boundary between Albany subtropical thicket and Nama-Karoo in South Africa. *J. Biogeogr.*, **42**: 167–178.

Dyer, T.G.J. 1976. Expected future rainfall over selected parts of South Africa. *S. Afr. J. Sci.*,

72: 237–239.

Dyer, T.G.J. 1975. Solar Activity and Rainfall Variation over Southern Africa. *S. Afr. J. Sci.*, **71**: 369–372.

Dyer, T.G.J. and Tyson, P.D. 1977. Estimating above and below normal rainfall periods over South Africa, 1972-2000. *J. Appl. Meteorol.*, **16**: 145–147.

Dyksterhuis, E.J. 1949. Condition and management of range land based on quantitative ecology. *J. Range Manag.*, **2**: 104–115.

Easterling, D.R., Horton, B., Jones, P.D., Peterson, T.C., Karl, T.R., Parker, D.E., *et al.* 1997. Maximum and minimum temperature trends for the globe. *Science.*, **277**: 364–367.

Ecker, M., Brink, J., Horwitz, L.K., Scott, L. and Lee-Thorp, J.A. 2018. A 12,000 year record of changes in herbivore niche separation and palaeoclimate (Wonderwerk Cave, South Africa). *Quat. Sci. Rev.*, **180**: 132–144.

Edwardes, A. 2018. The hydrological and ecophysiological effects of simulated climate warming on the soil and vegetation of the Nama Karoo. MSc Thesis. Stellenbosch University.

Edwards, D. 1984. Fire regimes in the biomes of South Africa. In: *Ecological Effects of Fire in South African Ecosystems* (P. de V Booysen and N. M. Tainton, eds), pp. 19–37. Berlin Heidelberg New York Tokyo: Springer-Verlag.

Egler, F.E. 1954. Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development. *Vegetatio*, **4**: 412–417.

Ellery, W.N., Scholes, R.J. and Mentis, M.T. 1991. An initial approach to predicting the sensitivity of the South African grassland biome to climate change. *S. Afr. J. Sci.*, **87**: 499–503.

Engelbrecht, F.A., McGregor, J.L. and Engelbrecht, C.J. 2009. Dynamics of the Conformal-Cubic Atmospheric Model projected climate-change signal over southern Africa. *Int. J. Climatol.*, **29**: 1013–1033.

Epstein, H.E., Lauenroth, W.K., Burke, I.C. and Coffin, D.P. 1997. Productivity patterns of C_3 and C_4 functional types in the U.S. Great Plains. *Ecology*, **78**: 722–731.

Erasmus, D., Phillips, L., Joubert, R., Burgess, M. and Coleman, A. 2012. First snowfalls of the season. *Farmer's Wkly.*

Esler, K.J., Milton, S.J. and Dean, W.R. 2006. *Karoo Veld Ecology and Management*. Briza.

Esque, T.C., Schwalbe, C.R., Haines, D.F. and Halvorson, W.L. 2004. Saguaros under siege: invasive species and fire. *Desert Plants*, **20**: 49–55. The University of Arizona.

Everson, C.S., Everson, T.M. and Tainton, N.M. 1985. The dynamics of *Themeda triandra* tillers in relation to burning in the Natal Drakensberg. *J. Grassl. Soc. South. Africa*, **2**: 18–25.

Forrester, J. 1988. Fire in the Karoo N.B.G. floral reserve. *Veld Flora*, **74**: 5–5.

Frasier, G.W. and Cox, J.R. 1994. Water balance in pure stand of Lehmann lovegrass. *J. Range Manag.*, **47**: 373–378.

Gelcer, E., Fraisse, C., Dzotsi, K., Hu, Z., Mendes, R. and Zotarelli, L. 2013. Effects of El Niño Southern Oscillation on the space-time variability of Agricultural Reference Index for Drought in midlatitudes. *Agric. For. Meteorol.*, **174**: 110–128.

Geldenhuys, C.J. 1994. Bergwind fires and the location pattern of forest patches in the southern Cape landscape, South Africa. *J. Biogeogr.*, 49–62.

Gentry, A.H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Missouri Bot. Gard.*, 1–34.

Germishuizen, G. and Meyer, N. 2003. Plants of southern Africa: an annotated checklist. *Strelitzia*, **14**: 1–1233.

Gertenbach, W.P.D. 1980. Rainfall patterns in the Kruger National Park. *Koedoe*, **23**: 35–43.

Gill, G.A. 1939. Camp No. 6 grazing experiment. Botanical report: season 1938-1939. Middelburg, Eastern Cape: Grootfontein Agricultural Development Institute Archives.

Google. 2014. Google Earth (Version 7.1.2.2041) [Computer program]. Available at http://www.google.com/earth/download/ge/agree.html. (Accessed 1 October 2014 - 15 May 2015).

Groenewald, G. 2011. *Palaeontological impact asessment report. The proposed rehabilitation of Section 7 of the N9 National Road. Middelburg, Eastern Cape Province South Africa*. East London.

Gu, D. and Philander, S.G.H. 1995. Secular changes of annual and interannual variability in the tropics during the past century. *J. Clim.*, **8**: 864–876.

Hall, M. 1976. Dendrochronology, rainfall and human adaptation in the Later Iron Age of Natal and Zululand. *South. African Humanit.*, **22**: 693–703.

Henig-Sever, N., Eshel, A. and Ne'eman, G. 1996. pH and osmotic potential of pine ash as post-fire germination inhibitors. *Physiol. Plant.*, **96**: 71–76.

Henschel, J.R. 2015. Locust times-monitoring populations and outbreak controls in relation to Karoo natural capital. *Trans. R. Soc. South Africa*, **70**: 135–143.

Herranz, J.M., Ferrandis, P. and Martinez-Sanchez, J.J. 1998. Influence of heat on seed germination of seven Mediterranean Leguminosae species. *Plant Ecol.*, **136**: 95–103.

Hetem, R.S., de Witt, B. a., Fick, L.G., Fuller, A., Kerley, G.I.H., Maloney, S.K., *et al.* 2009. Shearing at the end of summer affects body temperature of free-living Angora goats (*Capra aegagrus*) more than does shearing at the end of winter. *Animal*, **3**: 1025–1036.

Hewitson, B.C. and Crane, R.G. 2006. Consensus between GCM climate change projections with empirical downscaling: precipitation downscaling over South Africa. *Int. J. Climatol.*, **26**: 1315–1337.

Higgins, S.I., Bond, W.J. and Trollope, W.S.W. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *J. Ecol.*, **88**: 213–229.

Hobson, F.O. and Sykes, E. 1980. Defoliation frequency with respect to three Karoo Bush species. *Karoo Agric*, **1**: 9–11.

Hoffman, M.T. 1989. Vegetation studies and the impact of grazing in the semi-arid Eastern Cape. PhD Thesis. University of Cape Town.

Hoffman, M.T., Barr, G.D. and Cowling, R.M. 1990. Vegetation dynamics in the semi-arid eastern Karoo, South Africa: the effect of seasonal rainfall and competition on grass and shrub basal cover. *S. Afr. J. Sci.*, **86**: 462–463.

Hoffman, M.T., Bond, W.J. and Stock, W.D. 1995. Desertification of the eastern Karoo, South Africa: conflicting paleoecological, historical, and soil isotopic evidence. *Environ. Monit. Assess.*, **37**: 159–177.

Hoffman, M.T. and Cowling, R.M. 1990. Vegetation change in the semi-arid eastern Karoo over the last 200 years: an expanding Karoo-fact or fiction? *S. Afr. J. Sci.*, **86**: 286–294.

Hoffman, T. and Todd, S. 1999. Vegetation degradation. In: *Land Degradation in South Africa.* Cape Town: South African National Biodiversity Institute.

Holland, S.M. 2008. Non-metric multidimensional scaling (MDS). Department of Geology, University Of Georgia, Athens, GA.

Humphrey, R.R. 2015. The desert grassland, past and present. *Fire Ecol.*, **11**: 5–11.

Hunter, M.D. and Price, P.W. 1992. Playing Chutes and Ladders : heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, **73**: 724–732.

Huntley, B.J. 1984. Characteristics of South African Biomes. In: *Ecological Effects of Fire in South African Ecosystems* (P. de V Booysen and N. M. Tainton, eds), pp. 1–17. Berlin Heidelberg New York Tokyo: Springer-Verlag.

Jager, J.C. and Looman, C.W.N. 1987. Data collection. In: *Data analysis in landscape and community ecology* (R. H. G. Jongman, C. J. F. ter Braak, and O. F. R. Van Tongeren, eds), pp. 10–28. Wageningen: Pudoc.

Jones, F.E. and Esler, K.J. 2004. Relationship between soil-stored seed banks and degradation in eastern Nama Karoo rangelands (South Africa). *Biodivers. Conserv.*, **13**: 2027–2053.

Joubert, J. 1988. Fighting small stock diseases after rains. *Karoo Reg. Newsl.*, **1**: 1–2.

Jürgens, N. 2006. Desert Biome. In: *The vegetation of South Africa, Lesotho and Swaziland* (L. Mucina and M. C. Rutherford, eds), pp. 300–323. Pretoria: SANBI.

Jury, M.R. and Levey, K. 1993. The Eastern Cape drought. *Water SA*, **19**: 133–137.

Kane, R.P. 2009. Periodicities, ENSO effects and trends of some South African rainfall series: an update. *S. Afr. J. Sci.*, **105**: 199–207.

Keay-Bright, J. and Boardman, J. 2006. Changes in the distribution of degraded land over time in the central Karoo, South Africa. *Catena*, **67**: 1–14.

Kraaij, T. and Ward, D. 2006. Effects of rain , nitrogen , fire and grazing on tree recruitment and early survival in bush-encroached savanna , South Africa. *Plant Ecol.*, **186**: 235–246.

Kratsch, H.A. and Wise, R.R. 2000. The ultrastructure of chilling stress. *Plant, Cell Environ.*, **23**: 337–350.

Kruger, A.C. and Shongwe, S. 2004. Temperature trends in South Africa: 1960-2003. *Int. J. Climatol.*, **24**: 1929–1945.

Lamont, B.B., Enright, N.J. and He, T. 2011. Fitness and evolution of resprouters in relation to fire. *Plant Ecol.*, **212**: 1945–1957.

Lippitt, C.L., Stow, D.A., O'Leary, J.F. and Franklin, J. 2013. Influence of short-interval fire occurrence on post-fire recovery of fire-prone shrublands in California, USA. *Int. J. Wildl. Fire*, **22**: 184–193.

MacKellar, N., New, M. and Jack, C. 2014. Observed and modelled trends in rainfall and temperature for South Africa: 1960-2010. *S. Afr. J. Sci.*, **110**: 51–63.

Manry, D.E. and Knight, R.S. 1986. Lightning density and burning frequency in South African vegetation. *Vegetatio*, **66**: 67–76.

Markham, C.G. 1970. Seasonality of precipitation in the United States. *Ann. Assoc. Am. Geogr.*, **60**: 593–597.

Martinez-Vilalta, J. and Llorte, F. 2016. Drought-induced vegetation shifts in terrestrial ecosystems: The key role of regeneration dynamics. *Glob. Planet. Change*, **144**: 94–108.

Mason, S.J., Waylen, P.R., Mimmack, G.M., Rajaratnam, B. and Harrison, J.M. 1999. Changes in extreme rainfall events in South Africa. *Clim. Change*, **41**: 249–257.

Masubelele, M.L., Hoffman, M.T., Bond, W.J. and Gambiza, J. 2014. A 50 year study shows grass cover has increased in shrublands of semi-arid South Africa. *J. Arid Environ.*, **104**: 43–51.

Meadows, M.E. and Watkeys, M.K. 1999. Paleoenvironments. In: *The Karoo - Ecological patterns and processes* (W. R. J. Dean and S. J. Milton, eds), pp. 1–374. Cambridge: Cambridge University Press.

Meissner, H.H. 1982. Classification of farm and game animals to predict carrying capacity. In: *Farming in South Africa. Pamphlet series. C-3*, pp. 1–3. Pretoria: Government Printer.

Midgley, G.F., Rutherford, M.C., Bond, W.J. and Barnard, P. 2008. The heat is on ... impacts of climate change on plant diversity in South Africa. National Botanical Institute, South Africa.

Midgley, G.F. and van der Heyden, F. 1999. Form and function in perennial plants. In: *The Karoo: ecological patterns and processes* (W. R. J. Dean and S. Milton, eds). Cambridge University Press.

Midgley, J.J. 1996. Why the world's vegetation is not totally dominated by resprouting plants; because resprouters are shorter than reseeders. *Ecography (Cop.).*, **19**: 92–95.

Midgley, J.J. and Bond, W.J. 2001. A synthesis of the demography of African acacias. *J. Trop. Ecol.*, **17**: 871–886.

Mielke, P.W. 1991. The application of multivariate permutation methods based on distance functions in the earth sciences. *Earth-Science Rev.*, **31**: 55–71.

Milton, S.J. 1994. Growth, flowering and recruitment of shrubs in grazed and in protected rangeland in the arid Karoo, South Africa. *Vegetatio*, **111**: 17–27.

Milton, S.J. 1995. Spatial and temporal patterns in the emergence and survival of seedlings in arid Karoo shrubland. *J. Appl. Ecol.*, **32**: 145–156.

Milton, S.J. 1993. Studies of herbivory and vegetation change in Karoo shrublands. PhD Thesis. University of Cape Town.

Milton, S.J., Davies, R.A.G. and Kerley, G.I.H. 2004. Population level dynamics. In: *The Karoo - Ecological patterns and processes* (W. R. J. Dean and S. J. Milton, eds), pp. 1–374. Cambridge: Cambridge University Press.

Milton, S.J., Dean, W.R.J., Marincowitz, C.P. and Kerley, G.I.H. 1995. Effects of the 1990/91 drought on rangeland in the Steytlerville Karoo. *S. Afr. J. Sci.*, **91**: 78–84.

Milton, S.J., Dean, W.R.J. and Marincowitz, P. 1990. Effects of the 1990 / 91 drought on rangeland in the SteytlerviHe Karoo. **91**: 78–84.

Milton, S.J. and 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 J. Range Forage Sci.*, **11**: 18–26.

Moll, E.J. and Gubb, A.A. 1989. Southern African Shrublands. In: *The Biology and Utilization of Shrubs* (C. M. McKell, ed), pp. 145–175. San Diego: Academic Press.

Morgan, J.A., LeCain, D.R., Pendall, E., Blumenthal, D.M., Kimball, B.A., Carrillo, Y., *et al.* 2011. C_4 grasses prosper as carbon dioxide eliminates desiccation in warmed semi-arid grassland. *Nature*, **476**: 202–205.

Morignat, E., Gay, E., Vinard, J.L., Calavas, D. and Hénaux, V. 2015. Quantifying the influence of ambient temperature on dairy and beef cattle mortality in France from a time-series analysis. *Environ. Res.*, **140**: 524–534.

Mucina, L., Hoare, D.B., Lötter, M.C., du Preez, P.J., Rutherford, M.C., Scott-Shaw, C.R., *et* *al.* 2006. Grassland Biome. In: *The vegetation of South Africa, Lesotho and Swaziland* (L. Mucina and M. C. Rutherford, eds), pp. 349–437. Pretoria: SANBI.

Mucina, L., Jürgens, N., le Roux, A., Rutherford, M.C., Schmiedel, U., Esler, K.J., *et al.* 2006. Succulent Karoo Biome. In: *The vegetation of South Africa, Lesotho and Swaziland* (L. Mucina and M. C. Rutherford, eds), pp. 220–299. Pretoria: SANBI.

Mucina, L. and Rutherford, M.C. 2006. *The vegetation of South Africa, Lesotho and Swaziland.* Pretoria: South African National Biodiversity Institute.

Mucina, L., Rutherford, M.C., Palmer, A.R., Milton, S.J., Scott, L., Lloyd, J.W., *et al.* 2006. Nama-Karoo Biome. In: *The vegetation of South Africa, Lesotho and Swaziland* (L. Mucina and M. C. Rutherford, eds), pp. 324–347. Pretoria: SANBI.

Mucina, L., Rutherford, M.C. and Powrie, L.W. 2006. Vegetation Atlas of South Africa, Lesotho and Swaziland. In: *The vegetation of South Africa, Lesotho and Swaziland* (L. Mucina and M. C. Rutherford, eds), pp. 749–790. Cape Town: SANBI.

Muller, K., O'Connor, T.G. and Henschel, J.R. 2016. Impact of a severe frost event in 2014 on woody vegetation within the Nama-Karoo and semi-arid savanna biomes of South Africa. *J. Arid Environ.*, **133**: 112–121.

Myburgh, D.W. 1994. The response of farmers to the drought hazard in the Karoo environment. *GeoJournal*, **33**: 401–410.

NASA. 2014. Fire Information for Resource Management System. Available at: firms.modaps.eosdis.nasa.gov.

New, M., Hewitson, B., Stephenson, D.B., Tsiga, A., Kruger, A., Manhique, A., *et al.* 2006. Evidence of trends in daily climate extremes over southern and west Africa. **111**: 1–11.

Nicholson, S.E. 2001. Climatic and environmental change in Africa during the last two centuries. *Clim. Res.*, **17**: 123–144.

Nicholson, S.E. 1989. Long-term changes in African rainfall. *Weather*, **44**: 46–56.

Nicholson, S.E. 2000. The nature of rainfall variability over Africa on time scales of decades to millenia. *Glob. Planet. Change*, **26**: 137–158.

Nicholson, S.E. and Entekhabi, M.D. 1986. The quasi-periodic behavior of rainfall variability in Africa and its relationship to the Southern Oscillation. *Arch. Meteorol. Geophys. Bioclimatol. Ser. A*, **34**: 311–348.

Novellie, P.A. and Bezuidenhout, H. 1994. The influence of rainfall and grazing on vegetation changes in the Mountain Zebra National Park. *South African J. Wildl. Res.*, **24**: 60–71.

O'Connor, T.G. and Roux, P.W. 1995. Vegetation changes (1949-71) in a semi-arid, grassy dwarf shrubland in the Karoo, South Africa: influence of rainfall variability and grazing by sheep. *J. Appl. Ecol.*, **32**: 612–626.

Ogle, K. and Reynolds, J.F. 2004. Plant responses to precipitation in desert ecosystems:

integrating functional types, pulses, thresholds, and delays. *Oecologia*, **141**: 282–294.

Ojeda, F., Brun, F.G. and Vergara, J.J. 2000. Fire , rain and the selection of seeder and resprouter life-histories in fire-recruiting , woody plants. *New Phytol.*, **168**: 155–165.

Palmer, A.R. 1990. *Vegetation survey of the Carnarvon Experimental Station*. Pretoria: Agricultural Research Council, Grassland Institute.

Parr, C.L., Gray, E.F. and Bond, W.J. 2012. Cascading biodiversity and functional consequences of a global change-induced biome switch. *Divers. Distrib.*, **18**: 493–503.

Paula, S. and Pausas, J.G. 2008. Burning seeds: germinative response to heat treatments in relation to resprouting ability. *J. Ecol.*, **96**: 543–552.

Pausas, J.G., Bradstock, R.A., Keith, D.A. and Keeley, J.E. 2004. Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology*, **85**: 1085–1100.

Paysen, T.E., Ansley, R.J., Brown, J.K., Gottfried, G.J., Haase, S.M., Harrington, M.G., *et al.* 2000. Fire in western shrubland, woodland, and grassland ecosystems. *Wildl. fire Ecosyst. Eff. fire flora. Gen. Tech. Rep. RMRS-GTR-42-vol*, **2**: 121–159.

Peltier, J. 2016. LOESS Utility for Excel. Peltier Tech Blog. (http:// peltiertech.com/loess-utility-for-excel/) [accessed 9 September 2015].

Potts, A.J., Moncrieff, G.R., Bond, W.J. and Cowling, R.M. 2015. An operational framework for biome boundary research with examples from South Africa. *South African J. Bot.*, **101**: 5–15.

Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A. and Solomon, A.M. 1992. Special paper: a global biome model based on plant physiology and dominance, soil properties and climate. *J. Biogeogr.*, **19**: 117–134.

Quinn, G.P. and Keough, M.J. 2002. *Experimental design and data analysis for biologists*. Cambridge: Cambridge University Press.

Rahlao, S.J., Milton, S.J., Esler, K.J., Van Wilgen, B.W. and Barnard, P. 2009. Effects of invasion of fire-free arid shrublands by a fire-promoting invasive alien grass (*Pennisetum setaceum*) in South Africa. *Austral Ecol.*, **34**: 920–928.

Rao, M.P., Davi, N.K., D'Arrigo, R.D., Skees, J., Nachin, B., Leland, C., *et al.* 2015. Dzuds, droughts, and livestock mortality in Mongolia. *Environ. Res. Lett.*, **10**: 074012(1-12).

Read, J. and Hill, R.S. 1989. The Response of Some Australian Temperate Rain Forest Tree Species to Freezing Temperatures and Its Biogeographical Significance. *J. Biogeogr.*, **16**: 21–27.

Reich, B.M. 1961. Short duration rainfall intensity in South Africa. *South African J. Agric. Sci.*, **4**: 589–614.

Roche, C.J. 2004. "Ornaments of the Desert". Springbok Treks in the Cape Colony , 1774-1908. MA Thesis. University of Cape Town.

Roques, K.G., O'connor, T.G. and Watkinson, A.R. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *J. Appl. Ecol.*, **38**: 268–280.

Roux, P.W. 1960. [Photograph]. Unpublished image.

Roux, P.W. 1993. *Complete inventory of the Camp No.6 veld grazing experiment*. Middelburg, Eastern Cape.

Roux, P.W. 1966. Die uitwerking van seisonesreenval en beweiding op gemengde Karooveld [The effects of seasonal rainfall and grazing on mixed Karoo veld]. *Proc. Grassl. Soc. South. Africa*, **1**: 103–110.

Roux, P.W. 1963. Progress report 1962-1963 K-Gf. 1. Veld grazing experiment: Camp No. 6 (Apron veld). Middelburg, Eastern Cape: Grootfontein Agricultural Development Institute Archives.

Roux, P.W. 1965a. Progress report 1964-1965. K-Gf. 2. Veld grazing experiment: Seligman Old Block. (Flats). Middelburg, Eastern Cape: Grootfontein Agricultural Development Institute Archives.

Roux, P.W. 1965b. Progress report 1964-1965 K-Gf. 1. Veld grazing experiment: Camp No. 6 (Apron veld). Middelburg, Eastern Cape: Grootfontein Agricultural Development Institute Archives.

Roux, P.W. 1967a. Progress report 1966-1967. K-Gf. 2. Veld grazing experiment: Seligman Old Block (Flats). Middelburg, Eastern Cape: Grootfontein Agricultural Development Institute Archives.

Roux, P.W. 1967b. Progress report 1966-1967 K-Gf. 1. Veld grazing experiment: Camp No. 6 (Apron veld). Grootfontein Agricultural Development Institute Archives.

Roux, P.W. 1973. Research Project 1972-1973 K-Gf. 1. Veld grazing experiment: Camp No. 6 (Apron). Grootfontein Agricultural Development Institute Archives.

Roux, P.W. 1990. *Seligman Old Block grazing experiment*. Middelburg, Cape Province.

Roux, P.W. 1991. *Special report on Seligman Old Block grazing experiment*. Middelburg, Cape Province.

Roux, P.W. 1964. Summary of interim report K-Gf. 1. Report for year ending 30th June, 1964. Middelburg, Eastern Cape: Grootfontein Agricultural Development Institute Archives.

Roux, P.W. and Theron, G.K. 1987. Vegetation change in the Karoo Biome. In: *The Karoo Biome: a preliminary synthesis. Part 2 - vegetation and history*, pp. 50–69.

Roux, P.W. and Vorster, M. 1983a. Development of veld management research in the Karoo region. *Proc. Annu. Congr. Grassl. Soc. South. Africa*, **18**: 30–34.

Roux, P.W. and Vorster, M. 1983b. Vegetation change in the Karoo. *Proc. Annu. Congr. Grassl. Soc. South. Africa*, **18**: 25–29.

Roux, P.W., Vorster, M., Zeeman, P.J.L. and Wentzel, D. 1981. Stock production in the Karoo region. *Proc. Annu. Congr. Grassl. Soc. South. Africa*, **16**: 29–35.

Rowswell, D.I. 1985. Weather related danger regions in the Angora Groat Industry. *Karoo Agric*, **3**: 10–16.

Rutherford, M.C., Mucina, L. and Powrie, L.W. 2006. Biomes and bioregions of southern Africa. In: *The vegetation of South Africa, Lesotho and Swaziland. Strelitzia* (L. Mucina and M. C. Rutherford, eds), pp. 30–51. Pretoria: SANBI.

Rutherford, M.C., Powrie, L.W. and Husted, L.B. 2012. Plant diversity consequences of a herbivore-driven biome switch from Grassland to Nama-Karoo shrub steppe in South Africa. *Appl. Veg. Sci.*, **15**: 14–25.

Rutherford, M.C., Powrie, L.W. and Schulze, R.E. 1999. Climate change in conservation areas of South Africa and its potential impact on floristic composition: a first assessment. *Divers. Distrib.*, **5**: 253–262.

Rutherford, M.C. and Westfall, R.H. 1986. *Biomes of southern Africa: an objective categorization* (O. A. Leistner, ed). Pretoria: Botanical Research Institute, Departement of Agriculture and Water Supply.

Sage, R.F. and Kubien, D.S. 2003. Quo vadis C_4 ? An ecophysiological perspective on global change and the future of C4 plants. *Photosynth. Res.*, **77**: 209–225.

Sakai, a and Wardle, P. 1978. Freezing resistance of New Zealand trees and shrubs. *N. Z. J. Ecol.*, **1**: 51–61.

Sakai, A. 1965. Survival of Plant Tissue at Super-Low Temperature III. Relation between Effective Prefreezing Temperatures and the Degree of Front Hardiness. *Plant Physiol.*, **40**: 882–887.

Scholes, R.J., Bond, W.J. and Eckhardt, H.C. 2003. Vegetation dynamics in the Kruger ecosystem. In: *The Kruger Experience* (H. C. Biggs, J. T. du Toit, and K. H. Rogers, eds), pp. 242–262. Island Press.

Schreiner, O. 1883. *Story of an African Farm*. London: Chapman & Hall.

Schwilk, D.W. and Ackerly, D.D. 2005. Is there a cost to resprouting? Seedling growth rate and drought tolerance in sprouting and nonsprouting *Ceanothus* (Rhamnaceae). *Am. J. Bot.*, **92**: 404–410.

Scott, L. 1989a. Climatic conditions in southern Africa since the last glacial maximum, inferred from pollen analysis. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **70**: 345–353.

Scott, L. 1989b. Late Quaternary vegetation history and climatic change in the eastern Orange Free State, South Africa. *South African J. Bot.*, **55**: 107–116.

Scott, L. and Lee-Thorp, J. 2004. Holocene climatic trends and rhythms in southern Africa. In: *Holocene climatic trends and rhythms in southern Africa* (R. W. Battarbee, F. Gasse, and C. E. Stickley, eds), pp. 69–91. Dordrecht, The Netherlands: Kliuwer Academic

Publishers.

Scott, L., Neumann, F.H., Brook, G.A., Bousman, C.B., Norström, E. and Metwally, A.A. 2012. Terrestrial fossil-pollen evidence of climate change during the last 26 thousand years in Southern Africa. *Quat. Sci. Rev.*, **32**: 100–118.

Searle, K.R., Gordon, I.J. and Stokes, C.J. 2009. Hysteretic responses to grazing in a semiarid rangeland. *Rangel. Ecol. Manag. Manag.*, **62**: 136–144.

Seymour, C.L., Milton, S.J., Joseph, G.S., Dean, W.R.J., Ditlhobolo, T. and Cumming, G.S. 2010. Twenty years of rest returns grazing potential, but not palatable plant diversity, to Karoo rangeland, South Africa. *J. Appl. Ecol.*, **47**: 859–867.

Shaw, J. 1873. On the changes going on in the vegetation of South Africa through the introduction of the Merino Sheep. *J. Linn. Soc. London, Bot.*, **14**: 202–208.

Skinner, T.E. 1965. Save the Bushman Grass. *Farming in South Africa*, **41**: 1–4.

Sklenář, P., Kučerová, A., Macek, P. and Macková, J. 2012. The frost-resistance mechanism in páramo plants is related to geographic origin. *New Zeal. J. Bot.*, **50**: 391–400.

Šmilauer, P. 2002. WinKyst 1.0. Ceske Budejovice, Czech Republic.

Smith, F.R. 2000. Factors Affecting The Dynamics of Nama Karoo Vegetation. PhD Thesis. University of Natal, Pietermaritzburg.

Smith, F.R. and Yeaton, R.I. 2005. Mean annual rainfall and the population growth (1993-2002) and potential distribution of *Themeda triandra* in the shrubby vegetation of the southern Nama-Karoo. *South African J. Bot.*, **71**: 117–121.

Snyman, H.A. 2004. Short-term response in productivity following an unplanned fire in a semi-arid rangeland of South Africa. *J. Arid Environ.*, **56**: 465–485.

Snyman, H.A. and Cowling, R.M. 2004. Short-term influence of fire on seedling establishment in a semi-arid grassland of South Africa. *South African J. Bot.*, **70**: 215–226.

Snyman, M. and van Heerden, M. 2011. Can protective coats alleviate the effect of cold, wet and windy conditions on Angora goats? *Grootfontein Agric*, **11**: 1–18.

Snyman, M.A. 2014. South African sheep breeds : Namaqua Afrikaner. Grootfontein Agricultural Development Institute.

Software Systat Inc. 2001. Sigmaplot for Windows, version 7.0s.

Squires, V.R. and Trollope, W.S.W. 1979. Allelopathy in the Karoo shrub, *Chrysocoma tenuifolia*. *S. Afr. J. Sci.*, **75**: 80–89.

Stager, J.C., Ruzmaikin, A., Conway, D., Verburg, P. and Mason, P.J. 2007. Sunspots, El Niño, and the levels of Lake Victoria, East Africa. *J. Geophys. Res. Atmos.*, **112**: D15106.

Statpoint Technologies Inc. 2009. Statgraphics Centurion X version 16:17.

Stephens, S.L. and Moghaddas, J.J. 2005. Experimental fuel treatment impacts on forest structure, potential fire behavior, and predicted tree mortality in a California mixed conifer forest. *For. Ecol. Manage.*, **215**: 21–36.

Stuart-Hill, G.C. and Hobson, F.O. 1991. An alternative approach to veld condition assessment in the non-grassveld regions of South Africa. *J. Grassl. Soc. South. Africa*, **8**: 179–185.

Sturrock, K. and Rocha, J. 2000. A multidimensional scaling stress evaluation table. *Field methods*, **12**: 49–60.

Sun, F. and Yu, J.-Y. 2009. A 10-15-yr modulation cycle of ENSO intensity. *J. Clim.*, **22**: 1718–1735.

Ter Braak, C.J.F. and Šmilauer, P. 2002. CANOCO 4.5 Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca, New York.

Thresher, R.E. 2002. Solar correlates of southern hemisphere mid-lattitude climate variability. *Int. J. Climatol.*, **22**: 901–915.

Tidmarsh, C. 1951. *Pasture research in South Africa. Progress report No. 3. Veld management studies: 1934-1950*. Middelburg, Cape Province: Grootfontein College of Agriculture.

Tidmarsh, C. 1957. Veld management in the Karoo and adjacent sweet grassveld region. In: *Handbook for Farmers in South Africa. Volume III. Stock Farming and Pastures*, pp. 624–635. Pretoria: The Government Printer.

Tidmarsh, C. and Havenga, C. 1955. *The wheel-point method of survey and measurement of semi-open grasslands and Karoo vegetation in South Africa*. Pretoria: The Government Printer.

Tiver, F. and Andrew, M.H. 1997. Relative effects of herbivory by sheep , rabbits , goats and kangaroos on recruitment and regeneration of shrubs and trees in eastern South Australia. *J. Appl. Ecol.*, **34**: 903–914.

Tiver, F., Nicholas, M., Kriticos, D. and Brown, J.R. 2001. Low density of prickly acacia under sheep grazing in Queensland. *J. Range Manag.*, **54**: 382–389.

Todd, M.C., Washington, R., Cheke, R.A. and Kniveton, D. 2002. Brown locust outbreaks and climate variability in southern Africa. *J. Appl. Ecol.*, **39**: 31–42.

Todd, S.W. 2006. Gradients in vegetation cover, structure and species richness of Nama-Karoo shrublands in relation to distance from livestock watering points. *J. Appl. Ecol.*, **43**: 293–304.

Torrence, C. and Webster, P.J. 1999. Interdecadal Changes in the ENSO – Monsoon System. *Am. Meteorol. Soc.*, **12**: 2679–2690.

Trollope, W.S.W. 1978. Fire - a rangeland tool in southern Africa. In: *Proceedings of the First International Rangeland Congress* (D. N. Hyder, ed), pp. 245–247. Denver: Society for Range Management.

Trollope, W.S.W., Trollope, L.A. and Hartnett, D.C. 2002. Fire behaviour a key factor in the fire ecology of African grasslands and savannas. In: *Forest Fire Research & Wildland Fire Safety, Viegas (ed.)*, pp. 1–15. Rotterdam: Millpress.

Tyson, P.D. 1971. Spatial variation of rainfall spectra in South Africa. *Ann. Assoc. Am. Geogr.*, **61**: 711–720.

Tyson, P.D. and Dyer, T.G.J. 1975. Mean annual fluctuations of precipitation in the summer rainfall region of South Africa. *South African Geogr. J.*, **57**: 105–110.

Tyson, P.D. and Dyer, T.G.J. 1978. The predicted above-normal rainfall of the seventies and the likelihood of droughts in the eighties in South Africa. *S. Afr. J. Sci.*, **74**: 372–377.

van den Berg, L., du Toit, J.C.O., van Lingen, M. and van der Merwe, H. 2019. The effect of sheep farming on the long-term diversity of the vegetation of the Karoo - a review. *Grootfontein Agric*, **19**: 66–72.

van den Berg, L. and Kellner, K. 2005. Restoring degraded patches in a semi-arid rangeland of South Africa. *J. Arid Environ.*, **61**: 497–511.

van der Vijver, C.A.D.M., Poot, P. and Prins, H.H.T. 1999. Causes of increased nutrient concentrations in post-fire regrowth in an East African savanna. *Plant Soil*, **214**: 173–185.

Van Laer, E., Moons, C., Ampe, B., Sonck, B., Vangeyte, J. and Tuyttens, F. 2015. Summertime use of natural versus artificial shelter by cattle in nature reserves. *Anim. Welf.*, **24**: 345–356.

van Meerten, E.J. 1927. A study of 39 years' rainfall. *Farming in South Africa*, **2**: 177–178; 182.

van Rooyen, M.W. 2004. Functional aspects of short-lived plants. In: *The Karoo - Ecological patterns and processes* (W. R. J. Dean and S. J. Milton, eds), pp. 1–374. Cambridge: Cambridge University Press.

van Wilgen, B.W. 2013. Fire management in species-rich Cape fynbos shrublands. *Front. Ecol. Environ.*, **11**: e35–e44.

van Wilgen, N.J., Goodall, V., Holness, S., Chown, S.L. and McGeoch, M.A. 2015. Rising temperatures and changing rainfall patterns in South Africa's national parks. *Int. J. Climatol.*

Venter, J.C. and Mebrhatu, M.T. 2005. Modelling of rainfall occurrences at Grootfontein (Karoo, South Africa). *South African J. Plant Soil*, **22**: 127–128.

Villarreal, M.L., Norman, L.M., Buckley, S., Wallace, C.S.A. and Coe, M.A. 2016. Multi-index time series monitoring of drought and fire effects on desert grasslands. *Remote Sens. Environ.*, **183**: 186–197.

Vines, R.G. 1980. Analyses of South African rainfall. *S. Afr. J. Sci.*, **76**: 404–409.

Visser, N., Botha, J.C. and Hardy, M.B. 2004. Re-establishing vegetation on bare patches in the Nama Karoo, South Africa. *J. Arid Environ.*, **57**: 155–177.

Vorster, M., Botha, P. and Hobson, F.O. 1983. The utilization of Karoo veld by livestock. *Proc. Annu. Congr. Grassl. Soc. South. Africa*, **18**: 35–39.

Vorster, M. and Roux, P.W. 1983. Veld of the Karoo areas. *Proc. Annu. Congr. Grassl. Soc. South. Africa*, **18**: 18–24.

Wentzel, D. 1989. Practical measures for the control of coccidiosis in Angora goats. *Angora Goat Mohair J.*, **31**: 1–4.

Westoby, M., Walker, B. and Noy-Meir, I. 1989. Opportunistic management for rangelands not at equilibrium. *J. Range Manag.*, **42**: 266–274.

Wiegand, T., Jeltsch, F., Bauer, S. and Kellner, K. 1998. Simulation models for semi-arid rangelands of southern Africa. *African J. Range Forage Sci.*, **15**: 48–60.

Wiegand, T., Milton, S.J. and Wissel, C. 1995. A simulation model for shrub ecosystem in the semiarid Karoo, South Africa. *Ecology*, 2205–2221.

Wiegand, T., Snyman, H.A., Kellner, K. and Paruelo, J.M. 2004. Do grasslands have a memory: modeling phytomass production of a semiarid South African grassland. *Ecosystems*, **7**: 243–258.

Wildi, O. 2013. *Data analysis in vegetation ecology*, 2nd ed. Wiley-Blackwell.

Wilson, J.B., Gitay, H., Roxburgh, S.H., McG, W. and Tangney, R.S. 1992. Egler's concept of "Initial Floristic Composition" in succession: ecologists citing it don't agree what it means. *Oikos*, 591–593.

Woodward, F.I., Lomas, M.R. and Kelly, C.K. 2004. Global climate and the distribution of plant biomes. *Philos. Trans. R. Soc. B Biol. Sci.*, **359**: 1465–1476.

World Meteorological Organization. 2012. *Standardized Precipitation Index User Guide* (M. Svoboda, M. Hayes, and D. Wood, eds). Geneva.

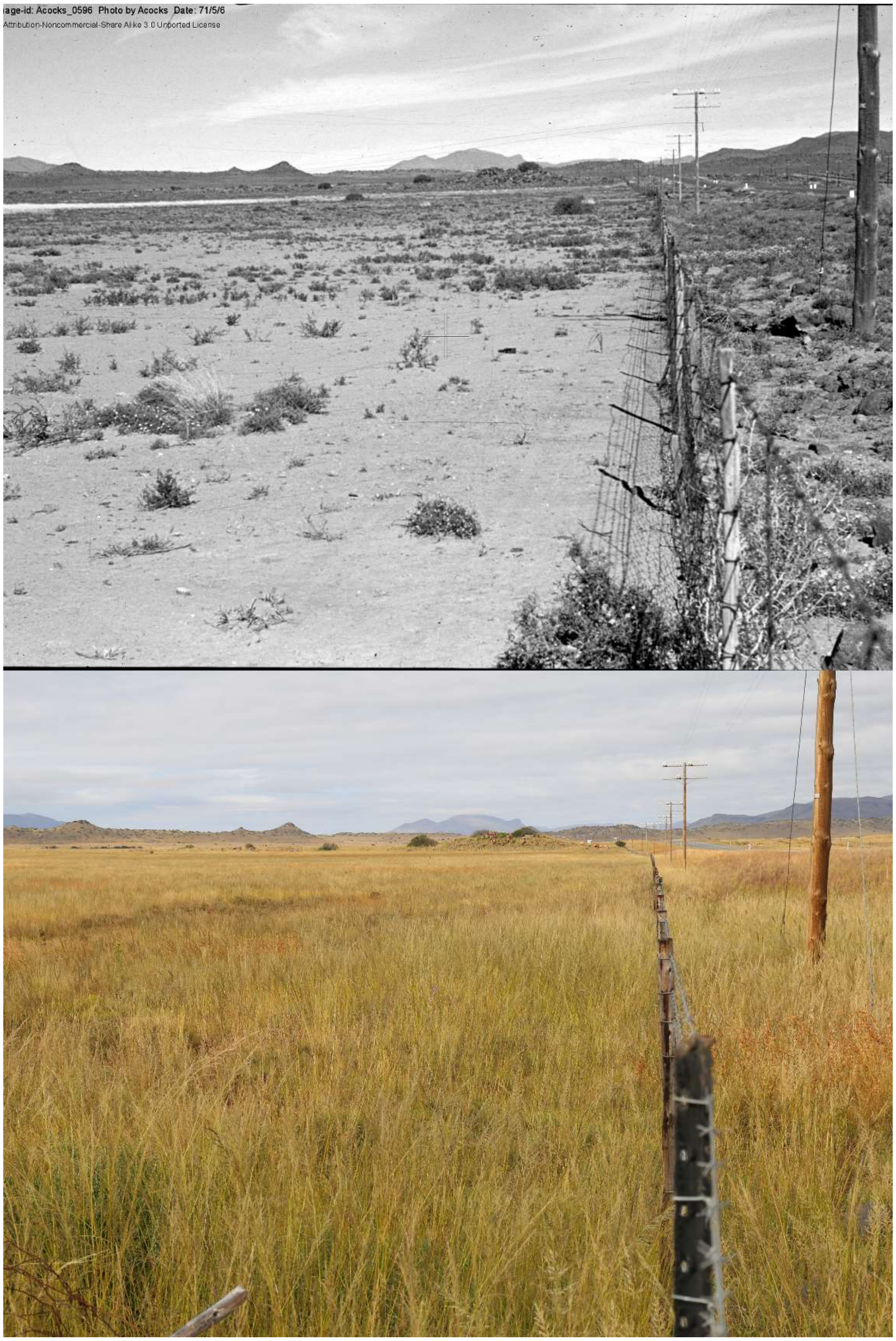
Zimmermann, J., Higgins, S.I., Grimm, V., Hoffmann, J. and Linstadter, A. 2010. Grass mortality in semi-arid savanna : The role of fire , competition and self-shading. *Perspect. Plant Ecol. Evol. Syst.*, **12**: 1–8.

Zimov, S.A., Chuprynin, V.I., Oreshko, A.P., Chapin III, F.S., Reynolds, J.F. and Chapin, M.C. 1995. Steppe-tundra transition: a herbivore-driven biome shift at the end of the Pleistocene. *Am. Nat.*, **146**: 765–794.

Zucchini, W. and Nenadić, O. 2006. A Web-based rainfall atlas for Southern Africa. *Environmetrics*, **17**: 269–283.

APPENDIX A. ADDITIONAL ILLUSTRATIVE INFORMATION

Unless specified, photographs presented in this appendix were taken by the author and are located in the Eastern Upper Karoo (Mucina, Rutherford, *et al.*, 2006).



Appendix A 1. Repeat photographs of a site approximately 11 km SSW of Middelburg taken by John Acocks in May 1971 [rephotosa.adu.org.za; accessed 1 April 2014)] and April 2016. The grasses in the bottom photograph are predominantly perennial tufted grasses such as *Sporobolus fimbriatus*, *Themeda triandra*, and *Eragrostis curvula*. Despite several intense short-term droughts, these grasses have persisted.

Appendix A 2. A flush of grass seedlings germinating following rain that broke a 4-month drought, the driest in 130 years. Most are probably *Aristida congesta*, *Aristida adscensionis*, or *Eragrostis lehmanniana*. This green flush is highly palatable to animals, and livestock will gain weight rapidly grazing this veld. Keys are for scale. Photo February 2019.

Appendix A 3. A near-monospecific stand of the large, tufted grass *Themeda triandra* (midground) at Camp 6, Grootfontein, with grassy shrubland in the foreground. Diversity in these patches is low, with the *Themeda* appearing to eliminate almost all other species. Mortality of individual tillers was high during short droughts, but most plants survived. Photo April 2013.

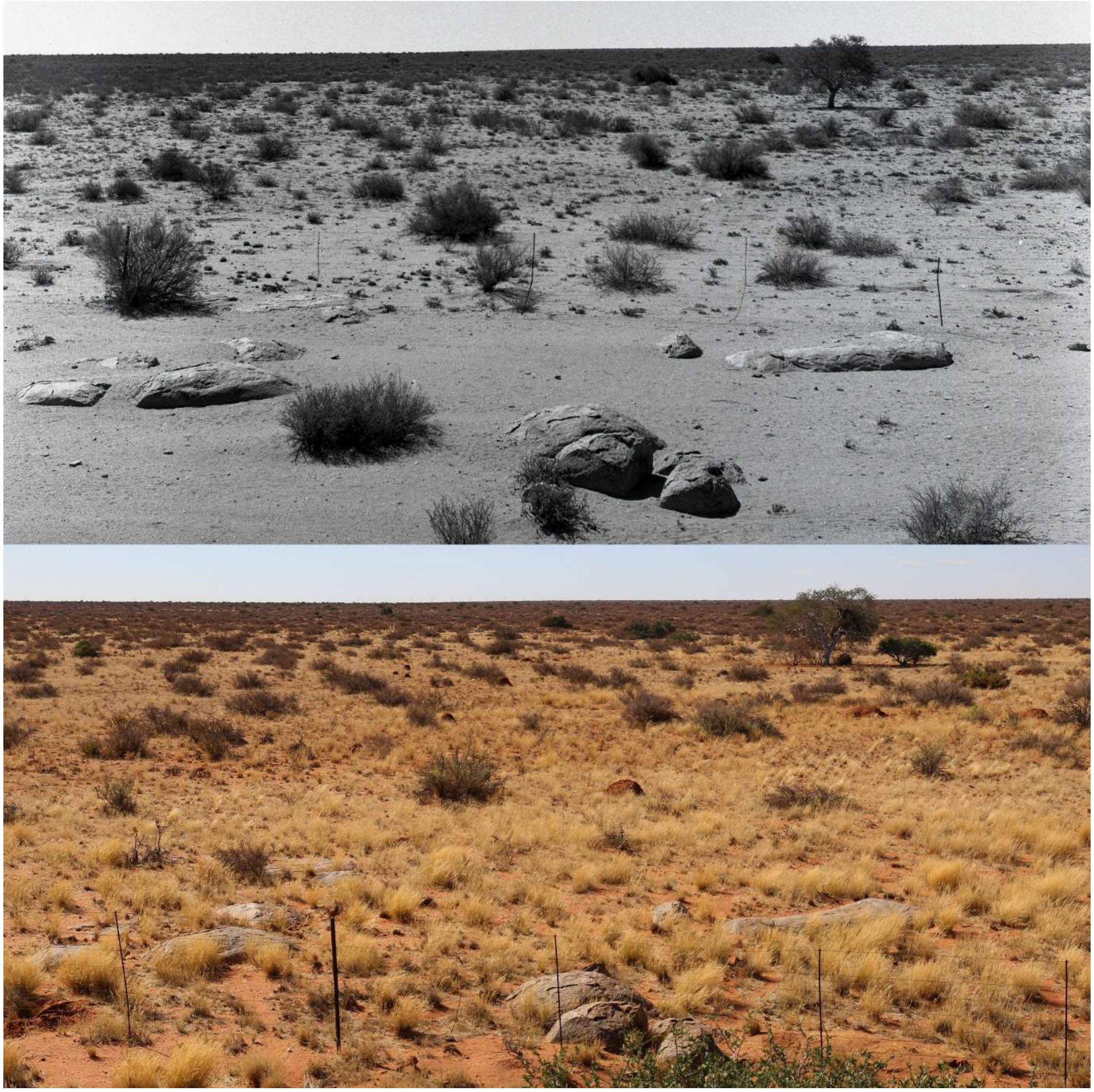
Appendix A 4. A nearly-dead tuft of *Aristida diffusa* following a short but severe drought. Most tillers are dead, but the plant will re-establish from the few survivors. This is a general pattern of grass mortality – although tiller death might be >95%, plant death can be <5%. Photo February 2019.

Appendix A 5. Repeat photographs at a site at Boesmanskop, Grootfontein, taken in January 2011 (top) following several years of above-average rainfall, and in November 2016 (bottom) following 6-month drought, showing the influence of rainfall variability on plant growth. Despite the obvious differences, species composition changed little over time, reflected mainly as a decrease in some *Eragrostis* species.

Appendix A 6. Two *Eriocephalus ericoides* plants of approximately the same size following a very dry period of four months. The plant on the left is dead (recently so, judging by the very thin branchlets still attached) while the one on the right has mainly dead branches but some that have produced leaves. Responses of shrubs to drought are currently poorly understood. Visual observations suggest that this resprouting species is shorter-lived than many re-sprouters. Photo February 2019.

Appendix A 7. Winter-only (left) and summer-only (right) grazing at the Bergkamp Research Trials in Besemkaree Koppies Shrubland at Grootfontein. Perennial grasses in the Winter treatment dominate, and are nearly absent in the Summer treatment. Large shrub density is also higher in the Summer treatment. Photo January 2011.

Appendix A 8. *Tragus koelerioides* plants after an intense 4-month drought that died (top) or nearly died but resprouted (bottom). This species rapidly colonises bare patches following a dry period. Annual congenerics also occur, but die out relatively quickly. Photos February 2019.



Appendix A 9. Repeat photographs of a site approximately 2 km SW of Putsonderwater in the Bushman Arid Grassland, Nama-Karoo Biome (Mucina, Rutherford, *et al.*, 2006) taken during a drought in November 1960 (top) (Roux, 1960) and in December 2016. The Karoo in general has seen an increase in grassiness over the past several decades, and while there are likely many drivers, it is probable that among these rainfall plays a major role.