

Factors limiting karoo shrub populations in the Nama-Karoo

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DEDICATION

This thesis is dedicated to my daughter, Ayla van Onselen.

Never be afraid to pursue your dreams and goals.

DECLARATION

I declare that this thesis is my own work. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted by me before for any other degree, diploma or examination at any other University or tertiary institution.

A handwritten signature in black ink, appearing to read 'Hebb', with a long horizontal stroke extending to the right.

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10 September 2023

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ABSTRACT

The Nama-Karoo Biome occupies the central and western region of South Africa. Nama-Karoo shrublands are dominated by karoo dwarf shrubs and in the wetter eastern regions annual and perennial grasses are interspersed among shrubs. Rainfall and grazing are the main drivers of vegetation change in the Nama-Karoo. Stocking rate, season of grazing and animal type are important influences on vegetation community composition, and rainfall determines shrub growth and the abundance of grass. More recently, fire has been identified as a driver of vegetation change. Understanding vegetation change is important for land managers in the Nama-Karoo as changes in karoo shrub communities have implications for forage availability. This thesis is focused on understanding how grazing, fire, grass-shrub competition, and soil moisture and temperature affect the composition, structure, growth and phenology of karoo shrubs in the Eastern Upper Karoo. Livestock type and stocking rate vary greatly over the greater Nama-Karoo area. Plant composition data from the Afrikaner-Hereford grazing trial at Grootfontein show that grazing has a strong legacy effect on Karoo rangelands and grazing-induced compositional and structural changes are clear many years after grazing has ceased. Different sheep breeds affect karoo shrub communities in different ways. There was a severe negative effect of heavy stocking with dorper sheep on karoo shrub communities and their structure; the impacts of merino sheep were significant but less severe. Effects of animal type and stocking rate were not consistent across the sites but appear to be dependent on edaphic factors. Soil physical properties appear to play an important part in determining the long term effects of grazing on karoo shrub communities.

Fire is a novel disturbance in the Karoo. Nine sites which had experienced fire for the first time in history were studied for the effect of fire on the composition and structure of their shrub communities. The immediate effect of fire on karoo shrub communities was severe and the legacy effect of fire was significant. The nature of recovery after a fire depended on the abundance of fire-intolerant obligate reseeder shrubs that are killed by fire compared to the abundance of fire-tolerant resprouting shrubs. Rainfall and grazing management were important determinants of shrub recovery after a fire. As rainfall increases, grass biomass is predicted to increase, and this may result in fire becoming a more frequent occurrence in the Nama-Karoo.

During periods of high rainfall, the biomass of grass in the Nama-Karoo increased at the expense of shrub cover. The effect of grass-shrub competition on shrub growth and phenology is not adequately explained by existing hypotheses of niche separation and succession. A field experiment which examined the growth and phenology of karoo shrubs in the presence of grass (unclipped control) and the absence of grass (grass removed by clipping) did not provide evidence of a competitive effect from grass on shrub growth or phenology. It did, however, provide valuable insight into how shrub growth and phenology are influenced by soil moisture and temperature.

Rainfall in the Nama-Karoo is sporadic and a karoo shrub's ability to utilise soil moisture will determine its ability to grow and successfully recruit. Shrub growth, with or without grasses in the vicinity, was strongly correlated with rainfall, but this was modified by temperature. Similarly, soil moisture and temperature were important for stem growth and phenology. Flowering occurred in response to soil moisture all year round but seeding occurred mainly during summer. Patterns of growth and phenology can be used by land managers to optimise shrub production while allowing phenological processes to take place.

The findings of this study provide further insight into how grazing, fire, competition, soil moisture and temperature influence shrub populations and their structure, and these are discussed in the context of an existing state-and-transition model for the Eastern Upper Karoo. The importance of animal type and stocking rate, and how they vary across Nama-Karoo landscapes, is highlighted. The legacy of both grazing and fire reveal that the transitions between the alternate states of Nama-Karoo shrublands are not easily reversed in a management timeframe. It may take decades for a community changed by grazing or fire, acting independently or in conjunction, to return to their former state even under benign management. These findings along with a description of how soil moisture and temperature influence shrub growth and phenology have been used to make ecologically sound recommendations for the management of Nama-Karoo rangelands.

Future research is needed to improve our understanding of how edaphic factors limit and influence karoo shrub populations across a variety of karoo landscapes, how repeat fires might change karoo vegetation, and whether temperature and the presence of pollinators influences shrub seed set. An assessment of the economic implications of vegetation change

in the Nama-karoo is warranted so that management recommendations can be made with both ecology and economy in mind.

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CHAPTER 1

Introduction

General Introduction

Vegetation changes in the Nama-Karoo, central South Africa, are described in several historic accounts from the early 1990s. Shifts in grass and shrub abundance were attributed to rangeland management and livestock farming practices. Over time, extended drought or periods of high rainfall together with rangeland management practices have emerged as the main drivers of vegetation change in the Nama-Karoo (Novellie and Strydom 1987, Hoffman and Cowling 1990, O'Connor and Roux 1995, Kraaij and Milton 2006, Mucina and Rutherford 2006). More recently fire and frost have been recognised as important disturbance factors in semi-arid Karoo vegetation (du Toit et al. 2015a, Muller et al. 2016).

Rainfall and drought induce ecological changes in Nama-Karoo shrublands (Dean et al. 1995). Drought tolerant species such as succulents and ephemerals can survive drought, while grasses are killed by drought particularly in the presence of grazing (O'Connor and Roux 1995, du Toit and O'Connor 2014). Shrubs can outcompete grasses during drought periods where they have access to deeper soil water (Osem et al. 2004, Letts et al. 2010). Similarly, prolonged periods of above-average summer rainfall may cause an increase in grassiness as C_4 grasses require more precipitation to flourish (Dickie and Parsons 2012, du Toit and O'Connor 2014, Masubelele et al. 2014). These changes ultimately alter competitive relationships between grass and shrubs and may lead to vegetation state change (Novellie and Strydom 1987, Westoby et al. 1989, Dean et al. 1995).

Current knowledge of vegetation change in the Nama-Karoo is based on changes in species composition and few studies have addressed the central question of how grazing, rainfall, frost, fire and competition affect Karoo shrub communities and the phenology of karoo shrub species. Without this understanding we are not able to accurately model and predict how vegetation state change takes place in the Nama-Karoo. Need for improved prediction has been heightened by the spectre of climate change. An observed trend over the past few decades is that an increased amount of summer rainfall (du Toit and O'Connor, 2014) has resulted in increased grassiness in the eastern regions of the Nama-Karoo (Masubelele et al., 2014). Although shrub-grass interaction has always defined the dynamics of Nama-Karoo vegetation (O'Connor and Roux, 1995; Roux and Vorster, 1983), the currently prevailing ecological environment differs markedly from any witnessed before. Karoo shrubs have now

been exposed to ongoing competition with grass, including grasses of greater stature than previously. Increased grassiness has resulted in a greater incidence of fire on Nama-Karoo plains (du Toit et al., 2015a). Fires may have long-term consequences which have yet to be determined. Changes in temperature regime including frost, which may have severe effects on vegetation (Muller et al., 2016), could manifest. But the importance of such novel interactions needs to be gauged in the context of the impact of long-present agents affecting vegetation dynamics, of which rainfall variability and herbivory are foremost.

The aim of this PhD is to determine factors affecting the abundance, distribution and phenology of karoo shrubs in the Eastern Upper Karoo. This study will contribute to significantly widening current scientific knowledge of the ecology of Karoo shrubs in an important livestock producing region of South Africa. Specific objectives of this study are to compare the community and phenotypic responses of Karoo shrubs to disturbances acting alone and in combination. I will define the effects of seasonal grazing regimes; varying animal stocking rates and animal type, fire, soil moisture, temperature and competition on the local-landscape distribution, density, and size structure of Karoo shrubs. Furthermore, I aim to describe the phenology of a subset of Karoo shrubs in terms of their growth, flowering and seeding.

Through improved understanding of Karoo shrub communities and their phenology, and in the context of climate change, I will describe the findings within this thesis in terms of land management and livestock ranching in the Eastern Upper Karoo.

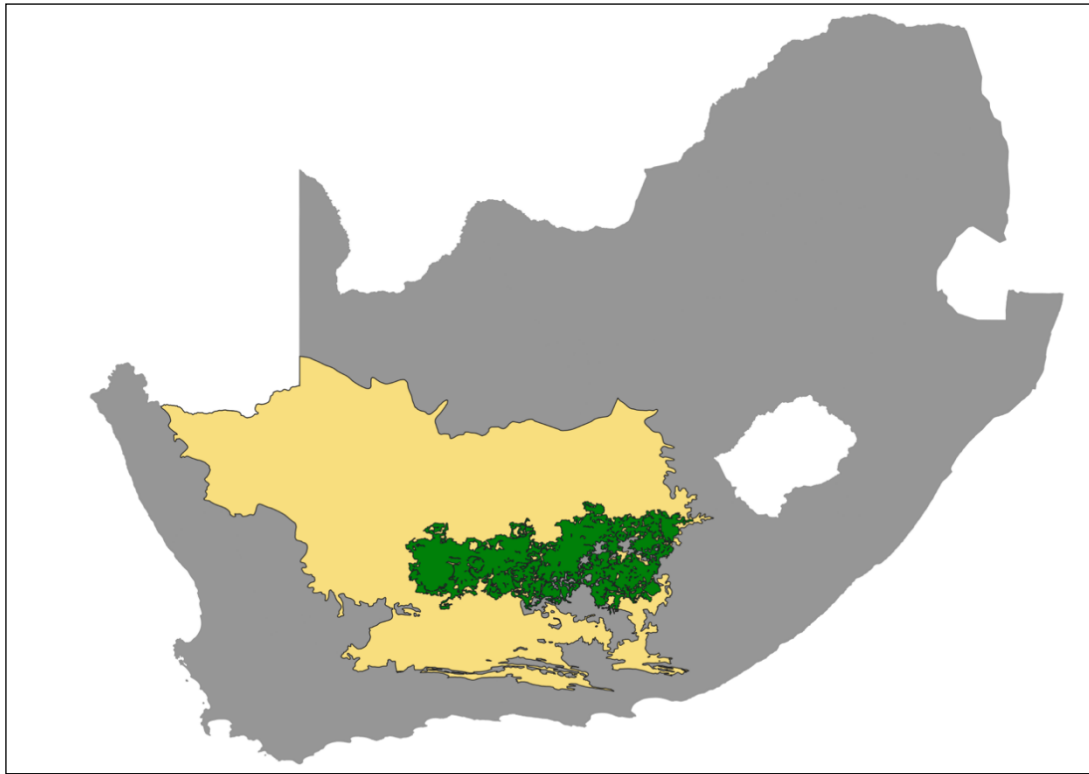


Figure 1. Location of the Nama-Karoo biome (yellow) in South Africa overlaid with the location of the Eastern Upper Karoo (green).

The Nama-Karoo

The Nama-Karoo is a dwarf, open and generally drought-deciduous shrubland consisting of mainly members of the Asteraceae, Poaceae, Aizoaceae, Crassulaceae and Fabaceae families with a conspicuous lack of tall woody trees, a characteristic attributed to a high frequency of frost (Duker et al., 2015; Mucina and Rutherford, 2006; Palmer and Hoffman, 1997). It is described as a relatively youthful biome that formed during the late Miocene in response to global cooling, regional aridification and local cooling associated with continental uplift. This suggests that the Nama-Karoo flora may be comprised of lineages that are pre-adapted to semi-arid, frosty climates (Mucina et al., 2006). The soils that cover most of the Nama-Karoo region are weakly developed lime-rich soils (Jones and Esler, 2004). These soils are principally underlain by sediments of the Dwyka Formation and are covered by the Ecce and Beaufort groups, which are exposed in some places as rocky outcrops (Groenewald 2011).

Extensive pastoralism and wildlife ranching are the primary economic activities in the biome (Hoffman and Cowling 1990, Shiponeni et al. 2011). Accounts of how these activities have driven vegetation changes in the Nama-Karoo have been described in several historic accounts from the early 1990s. Shifts in grass and shrub abundance were attributed to rangeland management and livestock farming practices and it was generally accepted that the Nama-Karoo was overstocked and thus degraded. However, over time extended drought or periods of high rainfall together with rangeland management practices emerged as the main drivers of vegetation change in the Nama-Karoo (Novellie and Strydom 1987, Hoffman and Cowling 1990, O'Connor and Roux 1995, Kraaij and Milton 2006, Mucina and Rutherford 2006). More recently fire and frost have been recognized as important disturbance factors in semi-arid Karoo vegetation (du Toit et al. 2014, Muller et al. 2016).

Karoo dwarf shrubs

Karoo dwarf shrubs, chamaephytes, are the dominant perennial flora of the Nama-Karoo. They seldom grow to heights of one metre and can be either succulent, leaf succulent or woody non-succulent. There is a great degree in variation between leaf size, shape, thorniness, woodiness and root structure of Karoo dwarf shrubs (Esler, 1999). Environmental stress has strongly influenced the selection of plant form in arid systems (Midgley and van

der Heyden, 1999). Life histories, drought resistance and palatability vary greatly among Karoo dwarf shrub species. Livestock show strong selection for species, with some species preferred and others avoided (du Toit et al., 1995; Midgley and van der Heyden, 1999). Karoo dwarf shrubs do not respond uniformly to herbivory and different species show markedly different growth responses to herbivory.

There is little information on the longevity of non-succulent Karoo dwarf shrubs (Milton et al., 1999). *Pteronia pallens* was aged using ring dating, based on this the longevity of the Karoo dwarf shrub is estimated to be 150 years (Milton et al., 1997). The longevity of other woody Karoo dwarf shrubs is expected to be extend over a century when compared with similar species that have been dated on the American continents (Milton et al., 1997). The growth of Karoo dwarf shrubs closely follows the availability of resources, primarily precipitation (Milton et al., 1997; Todd and Hoffman, 2009; Wiegand et al., 2000), although edaphic variation influences growth form and distribution over landscapes (Esler, 1999). Karoo shrub population growth depends on a number of variables including seed density, microsite quality and availability, soil moisture, runoff and transpiration (Milton et al., 1999). A large scale disturbance often precedes a large scale recruitment in the Nama-Karoo (Esler, 1999). Gaps created by drought, hail and trampling thereby decreasing competition may allow recruitment to take place.

Seedlings of non-succulent species appear to be less drought tolerant than succulent species (Yeaton and Esler, 1990). Recruitment is most successful in moist years, this results in a pattern of pulsed recruitment and is reflected in clumped distribution of shrub sizes over an area (Yeaton and Esler 1990; Esler 1999). Seedling survival is generally low. Seedlings are killed by frost (Donaldson, 1989), drought, herbivory and competition from existing vegetation (Milton, 1994).

Rainfall in the Nama-Karoo

Rainfall is a driver of vegetation change in semi-arid environments (Belsky 2008). Changes in rainfall patterns such as seasonal increases in rainfall or drought induce ecological changes (Dean et al., 1995). These changes have direct effects on species composition and interactions between plants (Richardson et al., 2005). Karoo shrubs do not respond to drought

uniformly. Some species are evergreen; others exhibit drought induced deciduousness (Esler, 1999). Drought favours drought tolerant species such as succulents (du Toit and O'Connor, 2014) and kills off grasses, particularly in the presence of grazing (O'Connor and Roux, 1995). Ephemerals including annual grasses thrive in the absence of competition for water or light. During a multi-year drought (2015-2019) in the eastern part of the Nama-Karoo there was no significant shrub mortality whereas mortality of grass tufts was observed (Archer et al 2022).

Similarly, prolonged periods of above-average rainfall may cause an increase in grassiness as C_4 grasses require more precipitation to flourish (Dickie and Parsons, 2012; du Toit et al., 2015b; du Toit and O'Connor, 2014; Masubelele et al., 2015). In addition to amount, seasonality of rainfall is important for shifts in the grassiness of Nama-Karoo rangelands (Archer et al 2022). In the Nama-Karoo the general understanding is that mid-summer rains promote C_4 grasses, while rains during other times of the year promote slower growing frost resistant C_3 shrubs (O'Connor and Roux, 1995).

Seasonality of rainfall in the Nama-Karoo shifts, where late rains are usually associated with lower rainfall amounts and early rains are associated with higher rainfall for the area (du Toit and O'Connor 2014). Grasses have benefited from recent increases in rainfall, increasing in abundance throughout the Nama-Karoo (Masubelele et al., 2015; O'Connor et al., 2011). Secondary effects of increased rainfall, and the resulting increase in grassiness, is the accumulation of flammable grass biomass which increases the likelihood of fires resulting in large disturbance events (du Toit et al., 2015a).

Arena et al (2023) found an increase in perennial grass cover in the Eastern Karoo, a trend attributed to the long-term increase in rainfall in the region. Similarly, they noted that the cover of palatable karoo shrubs had increased. Changes in grass and shrub abundance will change competitive relationships among plants relative to resource availability (Osem et al., 2004). Interactions between woody plants and grasses have been well studied, particularly in savanna ecosystems. The Karoo is like a savanna in that it is composed of C_4 grasses and C_3 woody shrubs but differs in the height and size of the woody shrub component. Fire shapes savanna vegetation communities and its effect on Nama-Karoo communities is unknown.

Research into interactions between Karoo shrubs and grasses is limited; however, it is generally predicted that higher rainfall would benefit grasses at the expense of shrubs, especially in the presence of fire (du Toit et al., 2015a). In contrast shrubs are expected to

flourish in the absence of fire and low rainfall, or during periods of drought (Archer et al 2022). Shrubs can outcompete grasses during droughts as their roots have access to deeper soil water (Letts et al., 2010). Furthermore, the growth of C₃ shrubs is positively influenced by higher concentrations of CO₂ in the atmosphere, this is due to their higher water use efficiency and growth rate (Morgan et al., 2007), while C₄ grasses show both a mixed response in growth rate at elevated CO₂ (Leakey et al., 2009; Morgan et al., 2011).

Long term rainfall data collected over 123 years at Grootfontein Agricultural Development Institute was analysed by du Toit and O'Connor (2014). They found a strong relationship between rainfall and season, where early rains are correlated with wet seasons. Furthermore, they found strong evidence of a 22-year rainfall cycle, which falls into a longer 100-year rainfall cycle. Rainfall is expected to decline in amount over the next 20 years, but we are unsure of the impact that climate change will have on these predictions.

With drought expected to occur approximately every 20 years it can be considered an important disturbance in Nama-Karoo ecosystems. Drought can have devastating effects on Karoo shrubs. Milton et al. (1990) found that during the 1990/1991 drought 75% of all shrubs in Baroe, near Steytlerville, died. The common species, *Eriocephalus ericoides* and *Pentzia incana*, were reduced by 95% and 78% respectively. After a drought during 1933 in Fauresmith 25% of all non-succulent shrubs, with the majority being *Pentzia incana* and *Rosenia humilis*, died (Milton et al, 1995). Leaf succulent species are more drought tolerant than non-succulent species (Milton et al., 1999, Milton et al., 2022) and show much lower mortality during droughts.

Grazing in the Nama-Karoo

Grazing is a major ecosystem driver and a widespread form of land use in arid and semi-arid rangelands (Belsky, 2008; Briske et al., 2003; Westoby et al., 1989). In the Nama-Karoo stocking rate, season of grazing and animal type are important influencers of vegetation community composition (du Toit et al., 2011; Fynn and O'Connor, 2000; Kraaij and Milton, 2006; O'Connor and Roux, 1995; Wiegand et al., 2000). If grazing changes the patterns of plant distribution through selective grazing which negatively affects plant demographic processes, e.g., seed production, dispersal, recruitment, and mortality or biotic interactions (Adler and Lauenroth, 2000; Briske et al., 2006; De Vries and Daleboudt, 1994) then it will change how an ecosystem functions by modifying the spatial patterns and structure of the

vegetation (Adler and Lauenroth, 2000). A consequence of these changes in vegetation composition is a reduction in carrying capacity and a decrease in agricultural production. Furthermore, spatial and temporal effects of grazing are compounded by other factors such as climate, disturbance and competition (Briske et al., 2003).

Grazing induced changes include a decrease in the density of palatable shrubs (du Toit et al., 2011; Fynn and O'Connor, 2000) and an increase in the relative abundance of unpalatable species and ephemerals (du Toit et al., 2011; Hoffman and Cowling, 1990). When damage caused by heavy grazing sets in it initially affects plant population demography, followed by a decline in diversity and productivity (Kraaij and Milton, 2006). If grazing causes a particular life stage to fail we would expect that that population would not be able to persist on the landscape (Magda et al., 2009). This has implications for each life stage, from flowering, seeding and recruitment to growth into adult life stages. Community level consequences of demography will determine whether a species response to disturbance enables it to persist or alternatively, become extinct in a community (Richardson et al., 2005). Extirpation of Karoo dwarf shrubs together with changes in rainfall may facilitate the establishment of grass, ephemeral and weed species resulting in a grassier vegetation state (Milton and Hoffman 1994).

Changes in species composition caused by grazing and browsing have been described in the Eastern Upper Karoo (Van den Berg, 2009) but there is a lack of knowledge about the different ways that grazing can affect other life stages and the demographic strategy of Karoo shrub populations (Magda et al., 2009). Milton (1994) found that grazing changed the demographic structure of populations in the arid Succulent Karoo. Ultimately the canopy volume of a shrub is reduced (Milton, 1994), resulting in decreased flower and seed production. Furthermore, selective grazing by sheep can lead to reduced seed production of some shrub species while leaving others intact (Milton and Dean 1990). Todd (2006) showed that Karoo shrubs with conspicuous palatable flowers were more likely to have reduced seed production and impaired reproductive ability because of florivory. Consumption by sheep can reduce seed production of palatable shrubs by 80-90% (Milton et al., 1999). If heavy grazing leads to reproductive failure it is most likely responsible for the decline in palatable species (Todd, 2006). Likewise the grazing of seedlings and saplings by domestic and wild herbivores prevents the regeneration of shrub populations (Hoffman et al., 2009).

The response of specific species to grazing has been described in some detail. Malan and Snyman (1995) showed that under controlled defoliation treatments the reproductive output of *Pentzia incana* significantly reduced. Hobson (1988) demonstrated that severely defoliated karoo shrubs cannot tolerate regular heavy defoliation. Malan (2015) found that the impact of defoliation frequency significantly decreased both above- and belowground phytomass production. Other species specific studies have shown how grazing affects individual plants. Stock et al. (1993) found that some Karoo shrubs respond to grazing by producing tannins and polyphenols. *Eriocephalus ericoides* shrubs do not show growth responses to heavy grazing, this decreases their survival ability under regular defoliation (van der Heyden and Stock 1995). *Osteospermum sinuatum* rapidly regrows after heavy grazing but this compensatory growth is only possible when enough water is available (van Heerden et al. 1996). Unfortunately, many of these responses have been tested in controlled greenhouse environments, and not in Nama-Karoo habitats (Malan, 2015).

Fire in the Nama-Karoo

Fire is rare in the Nama-Karoo and Karoo vegetation is not considered fire prone (du Toit et al. 2014, 2015). The shrub-dominated vegetation, low frequency of lightning strikes and low rainfall in the Nama-Karoo have meant that grassiness and combustible fuel load has remained low (Hoffman and Cowling, 1990). Although fires are uncommon in the Nama-Karoo, increased grassiness during years of good rainfall makes it important to explore how fire, as an extreme disturbance, affects Karoo vegetation. As rainfall has increased the Nama-Karoo has become grassier. Hoffman and Cowling (1990) describe the Grassland Biome as moving westwards encroaching into the eastern reaches of the Nama-Karoo. With increasing grassiness, the chance of fire increases. Fire is a sudden large disturbance event with the ability to transform landscapes as shown in many semi-arid northern hemisphere landscapes (Abatzoglou and Kolden, 2011; Lippitt et al., 2013) where such events will have large implications for species diversity and populations (Clarke et al., 2015).

During a recent period (2010 to 2014) high grass fuel load resulting from high rainfall meant that several fires were able to burn throughout the Nama-Karoo, specifically the Eastern and Northern Upper Karoo region (du Toit et al., 2015a, 2015b; Mucina et al., 2006; Rahlao et al., 2009). Understanding how fire changes Karoo vegetation is important as it is likely to have consequences for livestock farming, wildlife ranching and biodiversity. Particularly

since we know that grassiness is likely to fluctuate with rainfall patterns which are cyclical in the Karoo with 100 year and 22-year oscillations both observed and modelled (du Toit and O'Connor, 2014). Additionally, abundance of grass in arid and semi-arid rangelands is expected to increase as C_4 grasses become more water-use efficient and less prone to desiccation as atmospheric CO_2 increases (Midgley and Bond, 2015; Morgan et al., 2011).

Coexisting with grass the woody component of Karoo vegetation is similar to fire prone vegetation such as savanna where the survival of woody plants depends on their sensitivity to disturbance (Higgins et al., 2000). Grasses are more tolerant to fire than shrubs, with fire often playing an important role in the persistence of grasslands (Bond, 2008; Vesk and Westoby, 2004). The ability to escape fire, its sprouting ability and seedling establishment are important for savanna trees after fire. It is likely that the same characteristics will determine which Karoo shrub species can survive fire or return to the system through seedling establishment.

Plants in communities that experience devastating disturbance events follow two regeneration strategies; particularly when the disturbance results in the entire loss of the plant's canopy (Dalglish et al. 2012; Bond and Midgley 2001, Bond and Keeley 2005, Sardans et al. 2006, Van Wilgen 2013). The adults of species that are killed by fire are referred to as seeders or non-sprouters, whereas those that survive and regrow after fire are called sprouters (Bell, 2013; Schwilk, 2005). The impacts of a fire on sprouting species may be short lived whereas seeders can only return to the community through the germination of seed (Clarke et al., 2015; Van Wilgen, 2013). Sprouting species have buds underground or in their stems that allow them to regrow after fire (Del Tredici, 2001). Seeding species die after fire but their seeds which have been released into the system are able to germinate (Zammit and Westoby 2013, Snyman 2015).

Seeders rely solely on past seed production, favourable conditions for the germination and recruitment of these seeds and then the ability of young plants to persist amongst larger sprouting species and grasses. The demography of these species is severely impacted, and reproduction will only take place under a specific set of environmental conditions. At fire sites in the Nama-Karoo, seeding *Eriocephalus* species have been extirpated by fires with no evidence of recruitment many years after burning. A comparison between species present in adjacent burnt and unburnt sites five years after a burn at Boesmanskop at Grootfontein Agricultural Development Institute (Grootfontein) recorded no recruitment of seeding species

in burnt areas (du Toit et al 2015b). This suggests that the ability of seeders to recolonize burnt areas is poor and that fire, in that case, lead to extirpation of seeding species resulting in an alternate vegetation state where sprouting species and grass dominate (Havstad and James, 2010).

Seeding species are expected to produce many seeds which enter the system and germinate when gaps become available synchronously with resources required for germination. If germination fails after a large disturbance event then that species may not return to the system until the required conditions return. Germination after a fire is expected because of an increase in soil irradiance and a decrease in competition for water (Keeley and Fotheringham, 2000) but germination might fail for several reasons. Predation of seedlings in a pulsed germination event is likely to be high in the absence of an adult plant community, and fire might render the pH and osmotic conditions of the seedbed unfavourable for germination (Keeley and Fotheringham, 2000).

An important ecomorphological property that enables successful sprouting after fire is the presence of buds or pre-bud meristems that are located in plant parts that are sufficiently insulated to from the heat of a fire (Clarke et al., 2015; Pausas and Keeley, 2014). In order to sprout from surviving buds or meristematic tissue plants need a sufficient reserve of carbohydrates and nutrients (Bond and Midgley, 2003; Canadell et al., 2013; Vesk and Westoby, 2004). Furthermore, Bond and Midgley (2000) hypothesise that as atmospheric CO₂ increases sprouting species will grow faster after fire as the rate of carbohydrate accumulation and storage in woody plants is expected to increase.

Sprouting species have two advantages over seeders and seedling recruitment, 1) they are able to regrow immediately and 2) flowering can occur sooner. Sprouting species have improved access to resources after a fire (water, nutrients, light, and space) (Higgins et al., 2000; Lamont et al., 2011; Sardans et al., 2006), and therefore have a competitive advantage over seedlings. That competitive advantage is enhanced by having a well-developed root system. There is a conspicuous link between the dynamics of the level of buds and the level of individual plants that is important when examining the population biology of resprouting plants (Harper, 1977; Vesk and Westoby, 2004).

The role of fire, acting as a large disturbance event, in the transition from a Karoo shrubland to grassland will have significant effects on Karoo shrub populations, and their ability to persist in the Nama-Karoo. Preliminary evidence of this shift has been recorded

photographically and forms the motivation to conduct further detailed population studies on Karoo shrubs that have been burnt in the Eastern Upper Karoo (Mucina and Rutherford, 2006).

A list of sprouting and non-sprouting species was compiled for the Boesmanskop fire site at Grootfontein (du Toit et al., 2015b). Thirty-seven Karoo shrub species at the site were described as sprouters, these include both leaf succulent and non-succulent dwarf shrubs. Five shrubs were described as non-sprouters or seeders, these were *Eriocephalus ericoides*, *Eriocephalus spinescens*, *Ruschia intricata*, *Crassula subaphylla* and *Sarcocaulon salmoniflorum*. Thirteen species had unknown responses. Sixty seven percent of the Karoo shrub species occurring at the Boesmanskop site were described as sprouters which regrew after the fire suggesting that Karoo shrub populations will not be extirpated in fires, but that a change in Karoo shrub community composition and structure can be expected. The high proportion of sprouting species does not suggest that these species have evolved in response to fire as sprouting is almost ubiquitous to woody dicotyledonous plants (Pausas and Keeley, 2009).

du Toit, van den Berg and O'Connor (2015) noted that pre-fire shrub community composition determined post fire community composition and structure. Sprouting species regrow and non-sprouting species are either lost or become rare (du Toit et al., 2015b). Little is known about the long-term effects of fire on Karoo vegetation communities, but it can be assumed that in combination with grazing pressure there will be significant effects on the ecology of burnt vegetation communities.

Grass-shrub competition

Plant communities respond to density through either plasticity or mortality (Harper, 1977). Karoo shrubs and grasses co-exist in the Nama-Karoo in a similar manner to trees and grasses in savanna ecosystems where competitive and facilitative relationships exist between woody plants and grasses (Hoffman and Cowling, 1990). Globally semi-arid communities have been shown to be structured by competition. Insights into competition between Karoo shrubs are based mainly on interactions between succulent Karoo species (van Rooyen, 2016) where Carrick (2003) describes competition as more prevalent than facilitation.

A comprehensive view of plant competition needs to consider both the dynamics of the competing species or plant functional types and the dynamics of resources for which they

compete (Fowler, 2003). Competition and facilitation are important elements of plant vegetation structure and the coexistence of individuals in a community of semi-arid shrubs and grasses. Interference from neighbours affects the growth of plants in arid and semi-arid communities (Casper and Jackson, 1997; Fowler, 2003; Hamilton et al., 1999), and this growth can be further influenced by herbivory (Van Auken, 2000). This is because of the low stature, a relatively low plant density, high belowground biomass, and high root: shoot ratios (Cahill and Casper, 2000; Van Auken, 2000) of Karoo shrubs. Competitive ability of plants in arid and semi-arid communities depends on root biomass, root density, root branching, root radius, root hair characteristics, mycorrhizae, timing of growth and interactions with other soil organisms (Casper and Jackson, 1997).

Marginal competition between conspecifics in a Succulent Karoo community were attributed to differences in rooting systems (Carrick, 2003). Although the root systems of only a few Karoo shrubs have been described. Vertical root separation may facilitate the coexistence of succulent and non-succulent species as those investigated appear to show vertical separation in rooting strategies (Midgley and van der Heyden, 1999). Succulents tend to have shallower rooting systems than non-succulents allowing rapid response to water availability (Midgley and van der Heyden, 1999) suggesting that succulent, or leaf succulent, Karoo shrubs might compete in the same horizontal plane as grasses.

Density induced mortality or 'self-thinning' has not been observed in Karoo shrubs. Instead, biomass increased with density until a level is reached where the increase of biomass remains constant with any further increases in density (van Rooyen, 2004). In a planted experiment van Rooyen (2004) did not observe density induced mortality in a monospecific stand of Karoo dwarf shrubs. The response in the presence of other species is not known. Karoo shrubs seldom create closed canopy stands, a characteristic attributed to their slow growth in a semi-arid environment. It is likely that shrub-grass competition in the grassier Eastern Upper Karoo shrub-grass plays a greater role in plant community dynamics.

Two hypotheses have been presented to explain competition between grass and dwarf shrubs in the Eastern Karoo. Hoffman et al. (1990) and Milton and Hoffman (1994) proposed a cyclical model of succession in the eastern Karoo in which the swift response of grasses to high summer (or annual) rainfall results in a corresponding decline in Karoo shrubs. They suggest that morphological traits of grasses, their taller growth and shallow extensive root systems, enable grasses to out-compete Karoo shrubs for light and moisture. Alternately,

Roux (1966) argues that shrubs benefit from winter precipitation enabling them to recruit, grow and outcompete grasses. Both these hypotheses have been shown to be inadequate and are unlikely as O'Connor and Roux's meticulous analysis of long-term data for the region found little evidence for between-guild competition proposed by Milton and Hoffman (1994) or for the winter rain hypothesis as determinants of shrub cover suggested by Roux (1966). Unfortunately, neither of these studies directly tested competition between shrubs and grasses and are based on detailed observations of communities, highlighting the need to conduct fine scale field experiments to observe any competitive interactions between grasses and shrubs.

Summer rainfall influences competition between grasses and shrubs in the Nama-Karoo. When summer rainfall is higher than the long term mean grass cover increases at the expense of shrub basal cover (Hoffman and Cowling, 1990). Arena et al (2023) describe a westward expansion of grassland into the Nama-Karoo driven by an increase in mean annual rainfall and a reduction in livestock numbers. These factors have allowed grass density to increase although shrub diversity was described as remaining unchanged (Arena et al, 2023). If grassiness continues to increase in the Eastern Nama-Karoo and grasses are able to outcompete shrubs the result will be a transition of states from mixed grass-shrub vegetation to grass-dominated vegetation. For this reason, it is important to understand how changes in grassiness caused by rainfall changes, grazing and increasing atmospheric CO₂ will affect individual plants and the ability of populations to persist.

Aboveground competition for light is important in semi-arid shrub-grass communities (Krueger-Mangold et al., 2004). Small stature and slow growing individuals experience higher levels of competition for light in grass-shrub communities (Krueger-Mangold et al., 2004). Species turnover in the Nama-Karoo, and competition for light is expected to vary between different communities. Where the grass stand is dominated by short grass species such as *Aristida congesta* or *Tragus* species competition for light between shrubs and grasses will be low. In areas where tall tufted grasses such as *Digitaria eriantha* or *Themeda triandra* dominate, many small-stature shrubs will experience high levels of shading which may inhibit their photosynthetic ability and ultimately growth and reproductive abilities (Kambatuku et al., 2011; Sardans et al., 2006).

Above- and below ground competition can kill seedlings (Milton, 1994) which can limit populations by directly impacting the demography of species. Grasses inhibit the

germination, establishment, and growth of woody plants (Bush and Auken, 2008). An alternative is that shrubs and grasses play important facilitative roles in recruitment (Holmgren et al., 2012; Jankju, 2013). Some shrub species in the Succulent Karoo act as nurse plants for other shrubs and annuals, but only in the absence of herbivory (Milton et al., 1999). Facilitation has not been explored in Nama-Karoo communities.

In the Nama-Karoo, the most important resource is rainfall and soil moisture is widely accepted as the factor which determines competitive interactions between shrubs and grasses (Milton, 1992). Shrubs generally have deeper roots than grasses and it is widely accepted that shrubs can access water deeper in the soil profile. If moisture in deep soil layers is depleted, woody plants have been shown to employ the same strategy as grasses of spreading their roots laterally and occupying the upper soil layers (Hipondoka et al. 2003). This highlights the importance of the availability of water to each group of plants spatially and temporally and will be important in describing whether grasses will competitively exclude shrubs in the Nama-Karoo resulting in a transition from shrubland to grassland. If it is accepted that competition is not driven by niche partitioning and that shrubs and grasses are equally able to utilize water that enters the soil then water loss or the volume of precipitation received in a rainfall event may be the most important factor in competition between grasses and shrubs (Golluscio et al., 1998).

In a South American semi-arid shrubland Golluscio et al. (1998) cleared grasses from 30m² plots. Shrubs showed no growth response to rainfall events (normal or high) in normal rainfall years but showed significant growth when large rainfall events were experienced in a dry year, suggesting that the amount of water available may be more important. This is a significant observation in light of climate change predictions and an increased likelihood that a greater proportion of rainfall will occur as large distinct events instead of as regular small events (Heisler-White et al. 2003). Removal experiments demonstrate reciprocal competition between shrubs and grasses. The removal of one functional type should benefit the other functional type if they interact competitively (Fowler, 2003). The time of rainfall is important, if a species can start growing earlier in the season it will have an advantage over those that take longer to grow or reproduce.

Smith (2000) investigated competition in his PhD where he was able to identify interactions between selected grass and Karoo shrub species. He found competitive interactions between

shrubs and grasses depended on species composition in an area. Competition was found between *Digitaria argyrograpta* and *Eriocephalus spinosa* but not between *Eriocephalus ericoides* and *Digitaria argyrograpta* or between *Sporobolus ioclados* and *Rosenia humilis*. Most importantly he found a negative linear correlation between shrub growth and grass basal cover. Smith (2000) also found that shrubs affect flowering and tillering of grass plants but unfortunately did not investigate whether competition from grass limited flowering of Karoo shrubs. Smith (2000) highlighted that the sample of Karoo shrubs did not affect the growth of grasses, both seedlings and adults. Survival and growth experiments showed that shrubs did not affect the growth and survival of grass seedlings and adult tillers planted under their canopies. *Ruschia intricata* and *Eriocephalus spinescens* shrubs did not affect the growth of *Themeda triandra*. Likewise, *Pentzia globosa* did not affect the growth of *Eragrostis curvula*. Furthermore he found that all grasses transplanted under the canopy of *Lycium cinereum* grew well, producing many tillers and avoiding grazing by livestock highlighting the complexity of competitive and facilitative interactions in Karoo shrub communities.

Grass cover and community composition in the Eastern Upper Karoo is not uniform (du Toit and O'Connor, 2020). Annual grass and perennial tufted grasses dominate large or small patches. The life strategies of these grasses are important in considering how grasses and Karoo shrubs compete in the Eastern Upper Karoo (Milton, 1992).

State change in the Nama-Karoo

Climate, nutrient loading, habitat fragmentation and biotic exploitation can drive gradual changes in ecosystems. Natural systems are usually assumed to respond to these gradual changes in a smooth way. However, studies on lakes, coral reefs, oceans, forests and arid lands have shown that smooth change can be interrupted by sudden drastic change resulting in a contrasting state. Although the events that can trigger such shifts are diverse, recent studies have shown that a loss of resilience usually precedes a sudden transition to an alternate state. This suggests that strategies for sustainable management of such ecosystems should focus on maintaining resilience (Scheffer et al., 2001).

State change can be driven by disturbance (Sousa, 1984). Disturbance is a discrete event which leads to the death or damage of one or more individuals in a community which creates an opportunity for new individuals to establish (Sousa, 1984). An early description of

disturbance by Bender et al. (1984) distinguished between two different kinds of disturbances. The first, described as a 'pulse', is an instantaneous change in species numbers after which the community returns to its previous state. The second, described as a 'push', is a slow sustained alteration of species communities leading to a new community which exists at equilibrium (Bender et al., 1984). Later disturbance was described by Westoby et al (1989) as an event which results in a rapid transition between states, where a state is described by the species composition of the community (Westoby et al., 1989). This rapid change has been observed in the Eastern Upper Karoo where rare fires have resulted in a shift from a grassy shrubland to a sparse grassland over a short period (du Toit et al., 2015a). Gradual environmental changes or regular small deviations from the norm can disturb a community leading to change over time (Sousa, 1984). Climate change occurs more gradually over time usually resulting in a slow transition from one vegetation state to another. The Eastern Upper Karoo has experienced a slow transition to a grassier state in recent history due to an increase in rainfall (Masubelele et al., 2015).

Transitions between vegetation states are not always clearly defined and may only take place if a combination of factors act simultaneously on a community (Iglesias and Kothman, 1997; Westoby et al., 1989). Additionally, plant growth forms within vegetation communities might change, leading to changes in not only community composition but also structure (Mucina and Rutherford, 2006). Community level consequences of demography will determine whether a species response to disturbance and climate will enable that species to persist and dominate, or alternatively become extinct in a community (Richardson et al., 2005). Likewise, the characteristics and functioning of a community can change if there is a change in the relative proportion of different growth forms (Muller et al., 2016).

Vegetation models are used to predict changes in the state of vegetation or species demography. Linear models, also known as directional or successional models, describe vegetation change over time eventually ending in an unchanging climax state (Milton and Hoffman, 1994). In these models competition is the most important factor driving the change. Non-linear models, also known as cyclic and stochastic models, describe change over time as multiple steady states (Westoby et al., 1989). Cyclic models describe vegetation change as a result of changes in abiotic factors such rainfall and seasonality of rainfall or biotic factors such as competition and facilitation. Stochastic models such as state-and-transition models propose that changes in vegetation from one state to another are driven by unpredictable

climatic or disturbance events. In some cases, a combination of climatic influence and disturbance may lead to vegetation change (Westoby et al., 1989).

A state change of vegetation in the Eastern Upper Karoo may have a large impact on livestock farming practices and rangeland condition. A state-and-transition model developed for the semi-arid Nama-Karoo indicates a number of putative thresholds that facilitate an increase in shrubs through grazing (Cingolani et al., 2014; Milton and Hoffman, 1994). Transitions between vegetation states are not always clearly defined and may only take place if a combination of factors act simultaneously on a community (Westoby et al., 1989). Additionally, growth forms within vegetation communities might change, leading to changes not only in community composition but also community structure and plant growth form (Mucina and Rutherford, 2006). The proportion of growth forms or a particular species in a population has the potential to alter the functioning and character of a community (Muller et al., 2016). Growth form is an important and reliable indicator of associated traits in growth, plant longevity and palatability to livestock making. This is why the demography - how they reproduce, grow, and die - of Karoo shrubs is important (O'Connor and Roux, 1995). Likewise, a change in the cover or relative abundance of a representative species' growth form can change the character and functioning of a plant community (Muller et al., 2016).

Summary and outline

A state-and-transition model has been used to generate a hypothesis on transition and alternate states of vegetation in the eastern Nama-Karoo (Milton and Hoffman, 1994). The model only considers rainfall, grazing and mechanical clearing disturbances. The incorporation of fire and grass-shrub competition are necessary factors in describing transitions between ecological states of Nama-Karoo vegetation. Since the predictive insight of any model is constrained by the need for physiological and demographic data on species responses, the results from field observations and small-scale experiments will provide data to create better models for the region.

This study will focus on two aspects of shrub population dynamics. Firstly, the study aims to describe how the distribution and structure of shrub populations is affected by grazing, fire and competition, rainfall and temperature. Secondly, it aims to describe species-specific phenological responses to soil moisture and temperature. The findings of this study will

expand our understanding of the processes of vegetation in the Nama-Karoo and how the biome will respond to future management, environmental factors and climate change.

In order to explore these topics, a number of questions are posed and addressed in this thesis.

Question 1: How do livestock type and stocking rate, alone and in conjunction, impact karoo shrub communities in the Eastern Upper Karoo?

This question is addressed in Chapter 2 in a paper format (unpublished) that presents the botanical examination of two sites of the Afrikaner-Hereford grazing trial at Grootfontein. The influence of animal type (dorper and merino sheep) and stocking rate (low, intermediate and heavy) on shrub community composition, population structure, and the abundance of shrub functional types was examined.

Question 2: How does fire affect karoo shrub communities across a rainfall gradient under varying grazing intensities?

This question is addressed in Chapter 3 in a published paper that presents the results of a botanical examination of several fire sites throughout the Eastern Upper Karoo. The focus of this chapter was on how fire changed karoo shrub composition and structure along a west to east rainfall gradient under different grazing regimes. Special attention was paid to effects of fire on the abundance of fire-tolerant resprouting and fire-intolerant seeding species.

Question 3: Does reduced competition from grasses benefit Karoo shrubs?

This question is addressed in Chapter 4 in a published paper that presents the results of a field experiment conducted at Grootfontein. The growth and phenology of shrubs was measured over a year and compared between plots where grasses were regularly clipped to plots where no grass clipping was done. Although all grasses and Karoo shrubs were measured the study focused on the growth and phenology of the three most abundant species in the rangeland, *Eriocephalus ericoides*, *Eriocephalus spinescens* and *Ruschia intricata*.

Question 4: How does soil moisture and temperature influence karoo shrub growth phenology and growth?

This question is addressed in Chapter 4 in a published paper that presents the results of a field experiment conducted at Grootfontein. Changes in canopy cover, stem growth, flowering, budding and seeding of three common karoo shrubs, *Eriocephalus ericoides*, *Eriocephalus spinescens* and *Ruschia intricata* was monitored and compared to soil moisture and temperature over the period of one year.

** This thesis has been prepared and written in the format of scientific papers. The repetition of information, given this format, is unfortunately unavoidable but has been minimised as much as possible.*

**The referencing style in this thesis follows that of the journal “Journal of Arid Environments” or in the format of the journal in which the chapter was published.*

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CHAPTER 2

The impact of sheep grazing on shrub communities at the Afrikaner and Hereford grazing trials at Grootfontein in the Eastern Upper Karoo.

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Abstract

In the Nama-Karoo, grazing by livestock is an important driver of Karoo shrub composition. Many different breeds of livestock are farmed in the Nama-Karoo and stocking rate varies greatly over the region. In this study we examine how grazing by dorper and merino sheep applied at three stocking rates affected two Karoo shrublands on a long-term grazing trial at Grootfontein in the eastern Karoo. The effects of grazing treatment on shrub communities at the Afrikaner and Hereford sites of the Afrikaner-Hereford grazing trial differed greatly. At the sandier, grassier Afrikaner site, heavy grazing by dorper sheep had a significant effect on shrub composition, density and cover, whereas the effect of grazing treatment was less pronounced at the Hereford site. Lenient grazing by merino sheep resulted in a vastly different community compared to all other grazing treatments. Individual Karoo shrub species responded differently to grazing treatment. Overall shrub recruitment has faltered for all but three species, and populations were dominated by intermediate-sized and large individuals. Results indicate that grazing management, animal type and stocking rate are important determinants of Nama-Karoo rangeland composition and structure with evidence of a legacy effect which is longer than ten years.

Introduction

Grazing is a widespread form of land use in arid and semi-arid rangelands that is an important driver of ecosystems (Belsky, 2008; Briske et al., 2003; Westoby et al., 1989). Grazing can modify plant distributions and community structure through the influence of selective grazing on plant demographic processes such as seed production, seed dispersal, seedling establishment, and plant mortality (Adler and Lauenroth, 2000; Briske et al., 2006; De Vries and Daleboudt, 1994). Heavy grazing, particularly over long periods, can change community composition resulting in degradation of a rangeland (Westoby et al., 1989). If grazing causes a particular life stage to fail, we would expect that a population would not be able to persist on the landscape (Magda et al., 2009). Variables such as stocking rate, animal type, and animal distribution (grazing system) can all influence the sustainability of a grazing programme (Cingolani et al., 2014). The consequences of grazing-induced changes in vegetation composition and structure influence rangeland carrying capacity and the agricultural production and conservation potential of an area. Livestock stocking rate, grazing systems, and animal type are important influences on Nama-Karoo vegetation community composition (du Toit and O'Connor, 2020; Kraaij and Milton, 2006).

The semi-arid Nama-Karoo is a dwarf shrubland, interspersed with annual and perennial grasses, geophytes, and trees, that occupies the western interior of South Africa (Mucina et al., 2006). Ephemerals are abundant during the wet season. Grassiness in the Nama-Karoo fluctuates according to rainfall which is mainly received in the hot summer, with a smaller amount received in the cool, frost-prone winter (du Toit and O'Connor, 2016). The region has been used for extensive sheep farming of commercial breeds since the mid- to late 1700s (Archer, 2000). The value of the region as a livestock producing area resulted in an increase of livestock numbers which together with prolonged droughts, lead to widespread overgrazing and rangeland degradation. A decline in palatable grass and shrub species abundance and an overall reduction in plant cover were the two most notable features of overgrazed, degraded rangelands (Roux and Vorster, 1983; Vorster et al., 1987).

In a state-and-transition model for Nama-Karoo rangelands (Milton and Hoffman, 1994) grazing regimes which do not allow palatable species to recruit result in system dominated by unpalatable species. Despite this, they conclude that if such grazing regimes are removed, palatable species can return to the system. Furthermore, the model proposes that a prolonged

withdrawal of livestock from a system will enable it to return to a mixed rangeland with palatable species. The period over which these changes take place is unknown. This “legacy effect” is described as the inability of a rangeland to recover over an extended period of time (Cuddington, 2011). The legacy left by grazing on a rangeland has been attributed to soil chemistry (Beukes and Cowling, 2003), soil surface compaction, depletion of soil seed banks and the persistence of unpalatable shrubs (Roux and Vorster, 1983).

At a small scale, heavy continuous grazing management in the Nama-Karoo changes vegetation composition and soil properties (du Toit et al., 2011). Hobson (1988) demonstrated that the more severely plants are defoliated, the less frequently they can tolerate heavy defoliation. Later, Malan (2015) found that the impact of defoliation frequency significantly decreased both above- and belowground phytomass production.

The two most common livestock farmed in the Nama-Karoo are dorper and merino sheep. Long term grazing by dorper sheep is widely considered to be more damaging to Karoo rangelands than the long term grazing of merino sheep. Dorper sheep and merino sheep have different foraging behaviours (du Toit, 1988). Dorper sheep spend less time moving between grazing points compared to merino sheep, effectively spending more time at individual plants and thus removing relatively more plant matter from an individual than a merino sheep would (Brand, 2000). Return time to an individual plant is longer, such that in a large extensive area this might allow plants extended rest between browsing events. In a small area, where time between grazing events is shorter, plants may not have the time to recover. This may have a greater impact on the reproductive and growing potential of a plant than if it had been grazed by a merino sheep, which spends less time at each plant and removes less plant matter (du Toit et al 1995). Furthermore, dorper sheep are less selective and utilize a larger range of forage species (Brand, 2000; du Toit, 1988). Shrubs make up a lower proportion of the diet of merino sheep (65%) compared to dorper sheep (90%), although the pattern of selection changes according to season (du Toit, 1988). Overlap of diet between merino and dorper sheep is lowest during the wet season, when merinos include a larger proportion of ephemerals into their diet compared to dorper sheep (du Toit, 1988). Many shrubs flower in response to rain which is most common during summer and heavy browsing will negatively impact the reproductive potential of those plants.

Long-term controlled grazing experiments are a valuable approach for addressing the complexity of quantifying the spatial and temporal effects of grazing which are compounded by other factors such as chemical and physical soil characteristics, climate, disturbance and species competition (Briske et al., 2003). The Afrikaner-Hereford grazing experiment, which ran from 1988 to 2007, was established at Grootfontein Agricultural Development Institute (hereafter Grootfontein), in the Eastern Upper Karoo vegetation type of the Nama-Karoo Biome. Its purpose was to investigate the influence of stocking rate and small-stock animal breed on animal performance and vegetation composition. Such experiments, coupled with climatic data, provide useful insight into the long-term effects of grazing and the interaction of grazing and variability in inter-annual rainfall common in semi-arid areas. Since the impacts of grazing can persist for long periods in the Nama-Karoo, the experiment provides an opportunity to study the legacy effect of grazing Nama-Karoo vegetation after being destocked for over a decade.

Understanding the effects and interactions between stocking rate and livestock type is important because they are factors for which land managers can exert some control in affecting the long-term impacts of grazing on Nama-Karoo rangelands. The purpose of this study was to test the hypothesis that animal type and stocking rate applied to a Nama-Karoo rangeland is a determinant of Karoo shrub composition and the abundance of palatable and unpalatable species. The questions examined were:

- 1) Does livestock stocking rate affect mortality and regeneration of Karoo shrubs leading to changes in Karoo shrub community composition?
- 2) Are these changes influenced by livestock type?
- 3) Does livestock stocking rate affect the structure of Karoo shrub communities by changing Karoo shrub canopy cover, shrub density and shrub height?
- 4) Are changes in shrub community structure influenced by livestock type?
- 5) Do height distributions within shrub populations elucidate the effects of grazing management on population structure?

Methods and materials

Study site

This study was conducted Grootfontein (31°28'18" S, 25°01'33" E) in the Eastern Cape province of South Africa. Data were collected at the Afrikaner-Hereford Grazing trial. The mean annual rainfall at the site is 372 mm. Although seasonal rainfall at the site is variable,

the majority of rain falls between October and March (du Toit and O'Connor, 2014). During mid-summer (November to February), daily maximum and minimum temperatures range between 23°C and 30°C, and 10°C and 16°C, respectively. During mid-winter (June to August), maximum and minimum temperatures range between 10°C and 16°C and -4°C and 4°C, respectively, but regularly drop below -5°C, with an average of 62 frost nights per year (du Toit and O'Connor, 2016). Soils are shallow, weakly developed, lime-rich and sandy, and overlie sediments of the Beaufort Group Formation (Mucina et al., 2006).

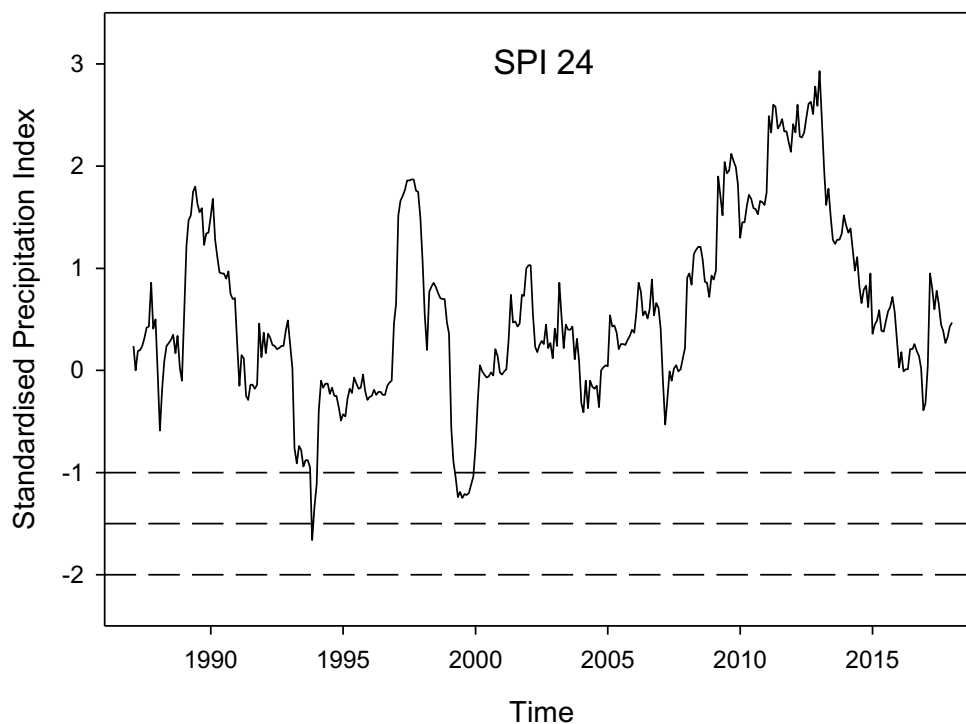


Figure 1: Standardised Precipitation Index values from 1987-2017, generated from a long-term dataset (1889-2021), for Grootfontein at a 24-month scale. Dashed lines represent Moderate (-1), Severe (-1.5), and Extreme droughts (-2) (du Toit J.C.O., unpublished data, 2022)

Trials and treatments

The Hereford-Afrikaner grazing trial was initiated in 1988 (Roux and Blom, 1988). The trial is made up of the Hereford site and the Afrikaner site situated approximately 5.1km apart. The Hereford site lies on gently sloping land of predominantly shallow (average depth of 269

mm) sandy loam and sandy clay loam soils that are rocky. The Afrikaner site lies on flatter land with predominantly deeper (average depth of 610 mm) sandy loam soils (unpublished data, M. van Lingen, Grootfontein Agricultural Development Institute). The trial was established to determine the optimum grazing capacity of Eastern Upper Karoo rangelands with different breeds of livestock. Identical treatments were applied at the Hereford and Afrikaner sites. Using nine paddocks per site, a fully randomised experimental design of three livestock stocking rates (1 ha/SSU (Small stock unit, High SR), 2 ha/SSU (Intermediate SR) and 3ha /SSU (Low SR)) for the three livestock breeds of merino sheep, dorper sheep, and, angora goats, with no replication of treatment combinations, was established (Figure 2).

Angora goats were removed from the treatments (A1, A2 and A3) before 2000 while the merino and dorper treatments continued until 2007. For this reason, the angora goat treatments were not examined in this study. Treatments were grazed for periods of four months by groups of each animal type, and these animals moved between the Afrikaner and Hereford sites until all remaining livestock were removed from the trial in 2007.

We recognise the small sample size and pseudoreplication in this study which will limit the wide applicability of our findings. Despite this we deem results to be a useful demonstration of grazing treatments in two Karoo shrubland communities.

Vegetation at the site is classified as Eastern Upper Karoo (Mucina et al., 2006). It is a shrubland dominated by microphyllous Karoo shrubs interspersed with grasses mainly of the *Eragrostis* and *Aristida* genera. Common Karoo shrub species at the Afrikaner grazing trial were *Eriocephalus ericoides*, *Selago geniculata*, *Pteronia tricephala* and *Trichodiadema setuliferum*. Common shrub species at the Hereford grazing trial were *Eriocephalus spinescens*, *Phymaspermum parviflorum*, *Selago geniculata* and *Eriocephalus ericoides*. Plant nomenclature follows SANBI (2019).

The Standardised Precipitation Index for the site shows that rainfall in the years after the removal of livestock from the trial and preceding this study was greater than the long-term average for the site (Figure 1).

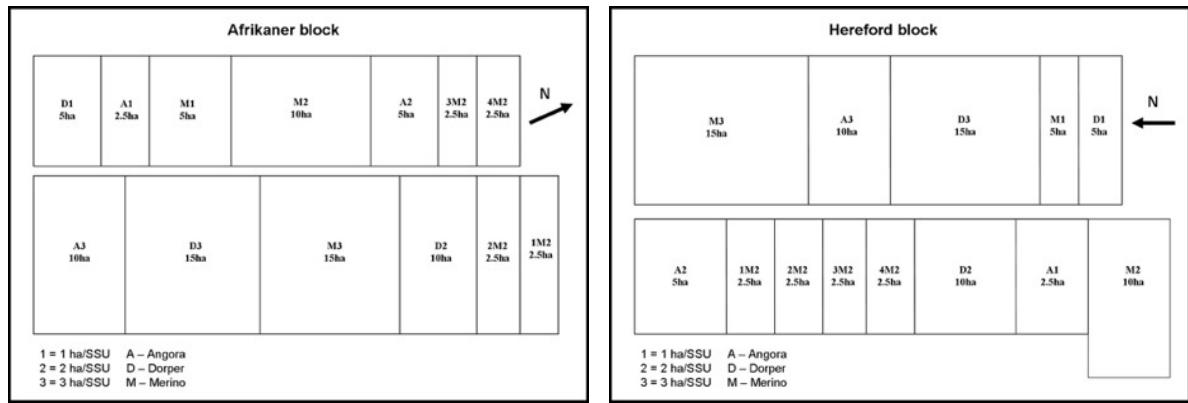


Figure 2: Schematic of the layout of the Afrikaner/Hereford Grazing Trial.

Data collection

Shrub community composition and structure were sampled at the Hereford and Afrikaner sites in April and May 2017. Twenty plots within each treatment were sampled. Plots within each treatment were stratified into four equal areas (strata) in a north to south direction. Using QGIS (QGIS.org, 2020), sample plot positions were randomly positioned within each stratum to ensure distribution of plots over the entirety of each paddock. Circular plots with a 1 m radius were sampled at the Hereford site, and plots with 2 m radius were sampled at the Afrikaner site. A larger plot size was used at the Afrikaner site on account of the lower shrub density at the site. All shrubs within a sample plot were identified and censused. Multi-stemmed plants were defined by the aggregation of their stems or visible vegetative anchoring common in some Karoo dwarf shrub species (Esler, 1999). Shrub height, the longest canopy diameter ($2r$) and the canopy diameter perpendicular to this ($2q$) were measured, and the proportion (L) of the shrub's canopy that had actively growing leaves was visually estimated. Plant canopy area (A) was defined as the area of the shrub with actively growing leaves and calculated as $A = \left(\pi \left(\frac{r}{2} \right) \left(\frac{q}{2} \right) \right) L$.

Grazing index values (GIV) were allocated to each species according to their capacity to produce fodder for livestock, seasonal nutritional quality, ease with which livestock can forage on a plant, life history strategy, and the capacity of an individual plant to protect the soil (Botha et al., 2001). Karoo shrubs with a $GIV < 4.25$ were classified as unpalatable and all shrubs with a $GIV \geq 4.25$ were classified as palatable in accordance with previous classification made by du Toit et al (2015). Karoo dwarf shrubs characterise Karoo

shrublands. Their low stature (<50 cm in height) and twisted woody stems distinguish them from other shrub species. The following karoo shrub functional types were recognised: Palatable dwarf shrub, Palatable succulent leaf dwarf shrub, Unpalatable dwarf shrub, Unpalatable parasitic dwarf shrub, Unpalatable true shrub (these are not dwarf shrub species), Palatable soft-stemmed dwarf shrub, Unpalatable soft-stemmed dwarf shrub, and unpalatable leaf succulent dwarf shrub. An assumption of such groupings is that between group variability exceeds within-group variability. Existing soil depth data for eight transects in each treatment (unpublished data, M. van Lingen, Grootfontein Agricultural Development Institute) collected in 2017 were used in the analyses. Tables and figures referring to shrubs include all functional types unless individual functional types are labelled.

Statistical analyses

Community response to grazing treatment is expressed as changes in composition and abundance. These multivariate responses can be quantified using multivariate techniques (McCune, 2002). Canonical Correspondence Analysis was undertaken, using the vegan package in Rstudio (Allaire, 2016; Oksanen et al., 2015), to analyse composition data to examine the effects of animal type, stocking rate and the interaction between animal type and stocking rate on shrub composition at each grazing trial. There was a slight variation in soil depth across the area of each grazing trial. Soil depth is known to influence vegetation composition (du Toit et al., 2018) but since it is an extraneous variable and cannot be effectively controlled in the experiment it was included in the analysis as a covariate (Yang and Juskiw, 2011). Owing to differences in species composition and environmental variables, data from the Afrikaner and Hereford sites were analysed separately to examine the effects of livestock stocking rate and livestock type on vegetation composition. Species that occurred in fewer than two strata were excluded from the analysis. Ordination plots were created in Rstudio (Allaire, 2016) using the ggplot2 package (Wickham, 2016).

The cover of all shrubs, palatable and unpalatable shrubs, functional types and common species were explored using analysis of covariance (ANCOVA) in Rstudio (Allaire, 2016) using the car package (Fox and Weisberg, 2019) with stocking rate and animal type as main effects, an interaction between stocking rate and animal type, and with the inclusion of soil depth as a covariate. Interaction plots were created in Rstudio (Allaire, 2016) using ggplot2 (Wickham, 2016).

A good indicator of grazing legacy is variation in plant height of a plant population. Accordingly, we used mixture models to examine the size (by height) structure of common shrub species in each treatment. Mixture models make no assumptions about the expected size distribution of individuals in the population (McLachlan and Peel, 2000). We assumed that patterns of size distribution within the shrub population were caused by recruitment, mortality or grazing pressure which prevents plants from reaching their potential height. The states described for an individual species, for each treatment, portray the main pattern of variation in plant size of that species within each treatment.

Stark differences in population size and structure are a consequence of the life history of that species but variations for a species across treatments can indicate important implications of those treatments on a specific species. Variations in the number of size distributions and the proportion of plants in each distribution can indicate patterns of recruitment or mortality, furthermore the absence or presence of plants of specific sizes, can indicate treatment specific impacts.

Mixture models use individual observations to determine size classes and can therefore be used to examine small populations with confidence. For species with more than 20 individuals in more than 80% of the treatments at each trial, a mixture model using a Weibull distribution was fitted. Minimum sample size enabled us to select species that were distributed throughout the treatments so comparisons on the effect of grazing and animal type could be made. The number and proportion of states chosen were based on Akaike's Information criterion (AIC). The output identifies the number of states, the physical nature of the state, the proportion of individuals in a particular state, and the mean height of each state. Mixture models were carried out in Rstudio (Allaire, 2016) using the ForestFit package (Teimouri, 2021). Each state represents a grouping of similar sized individuals within each population. The dominant state is the state in which the largest proportion of individuals is found. Where the ecologically appropriate number of distributions differed from model selection, an ecologically appropriate number of distributions was applied.

Results

Shrub community composition

The canonical correspondence analysis (CCA) for the Afrikaner site accounted for 52% of the species variance (Table 1) and demonstrated that there was a significant interaction effect

of stocking rate and animal type on the overall ordination and on its first axis (Figure 3, Table 2). This interaction effect showed that dorper and merino sheep had a markedly different effect on community composition at a high but not at a low stocking rate. Furthermore, there was a significant effect of stocking rate on community composition but no significant effect of animal type. High stocking rate (hereafter SR) treatments had a notably different composition compared to their respective intermediate and low SR treatments. There was no significant difference in species richness between treatments in the trial ($F_{1,2}=0.417$, $P=0.526$). The low and intermediate SR merino treatments were dominated by *Eriocephalus ericoides*. The high SR merino treatment was dominated by the unpalatable species *Pteronia glauca*, *Pteronia tricephala*, *Lycium cinereum* and *Selago geniculata* and two palatable species, *Pteronia sordida* and *Felicia muricata*. The high SR dorper treatment was dominated by the unpalatable species *Helichrysum rutilans*, *Helichrysum zeyheri*, *Senecio* sp., *Hertia pallens*, *Rosenia humilis* and *Wahlenbergia tenella*, and one palatable species *Osteospermum sinuatum* which was found only in this treatment.

The CCA for the Hereford site accounted for 44% of the species variance (Table 1) and demonstrated that animal type, stocking rate and the interaction between them significantly affected shrub community composition at the site (Figure 4, Table 2). Grazing by dorper sheep at high SR and at low SR resulted in significantly different communities that do not resemble communities grazed with merino sheep at the same stocking rates. There was no significant difference in species richness between treatments in the Hereford site ($F_{1,2}=0.391$, $P=0.682$). Three species, *Plinthus karroicus*, *Pentzia incana* and *Helichrysum lucilioides*, were abundant in the high SR dorper treatment. Palatable species *Osteospermum sinuatum*, *Melolobium candicans* and *Drosanthemum hispidum* were associated with the low SR dorper treatment. The intermediate SR merino treatment had a similar species composition with relatively few species being associated with those plots (Figure 4). The unpalatable leaf succulent shrub *Ruschia intricata* was common in merino treatments but absent in dorper treatments

Table 1: Summary Statistics of Canonical Correspondence Analysis

	Afrikaner		Hereford	
	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues	0.4931	0.2116	0.1197	0.0838
Cumulative % variance				
species data	19	34	10	18
Species-environment correlation	52	96	44	75

Table 2: Test statistics for first and all axes, and for environmental variables based on Monte-Carlo permutation tests (499 permutations).

	Afrikaner		Hereford	
	F ratio	P value	F ratio	P value
Test of significance of canonical axes				
First	5.6593	0.002	2.5540	0.013
All	4.6665	0.001	1.7875	0.109
Canonical coefficients				
Stocking Rate	4.3024	0.001	1.8123	0.023
Animal Type	1.8148	0.084	1.7164	0.023
Animal Type: Stocking Rate	4.6725	0.001	2.2795	0.001

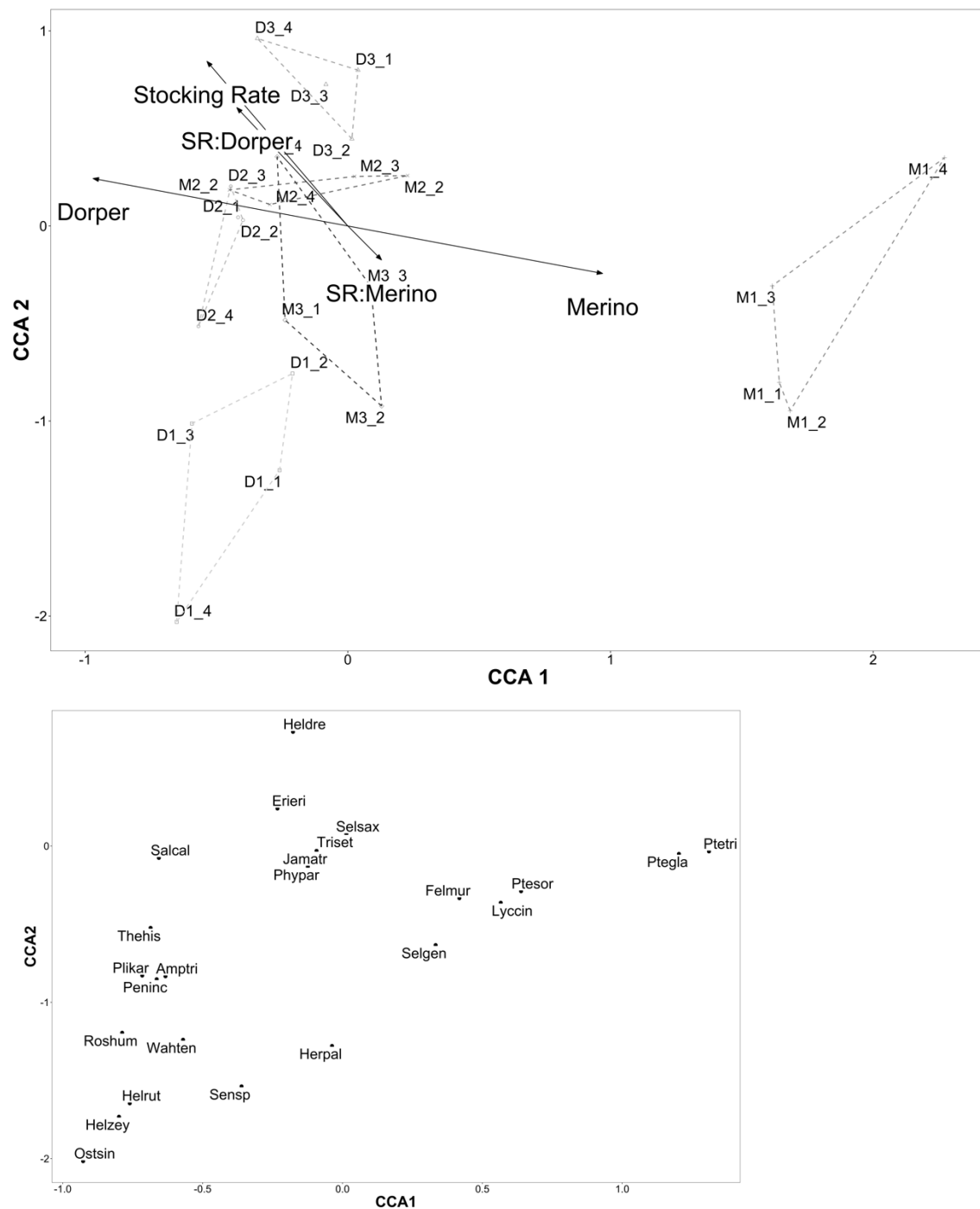


Figure 3: Canonical Correspondence analysis of vegetation composition and species distribution, using average shrub canopy cover, in each stratum (one quarter section of each treatment) within each treatment at the Afrikaner site of the Afrikaner-Hereford grazing trial. Points are labelled according to the trial, livestock breed, stocking rate and stratum number e.g. D1_1 = dorper sheep stocked at 1 ha/SSU, stratum 1.

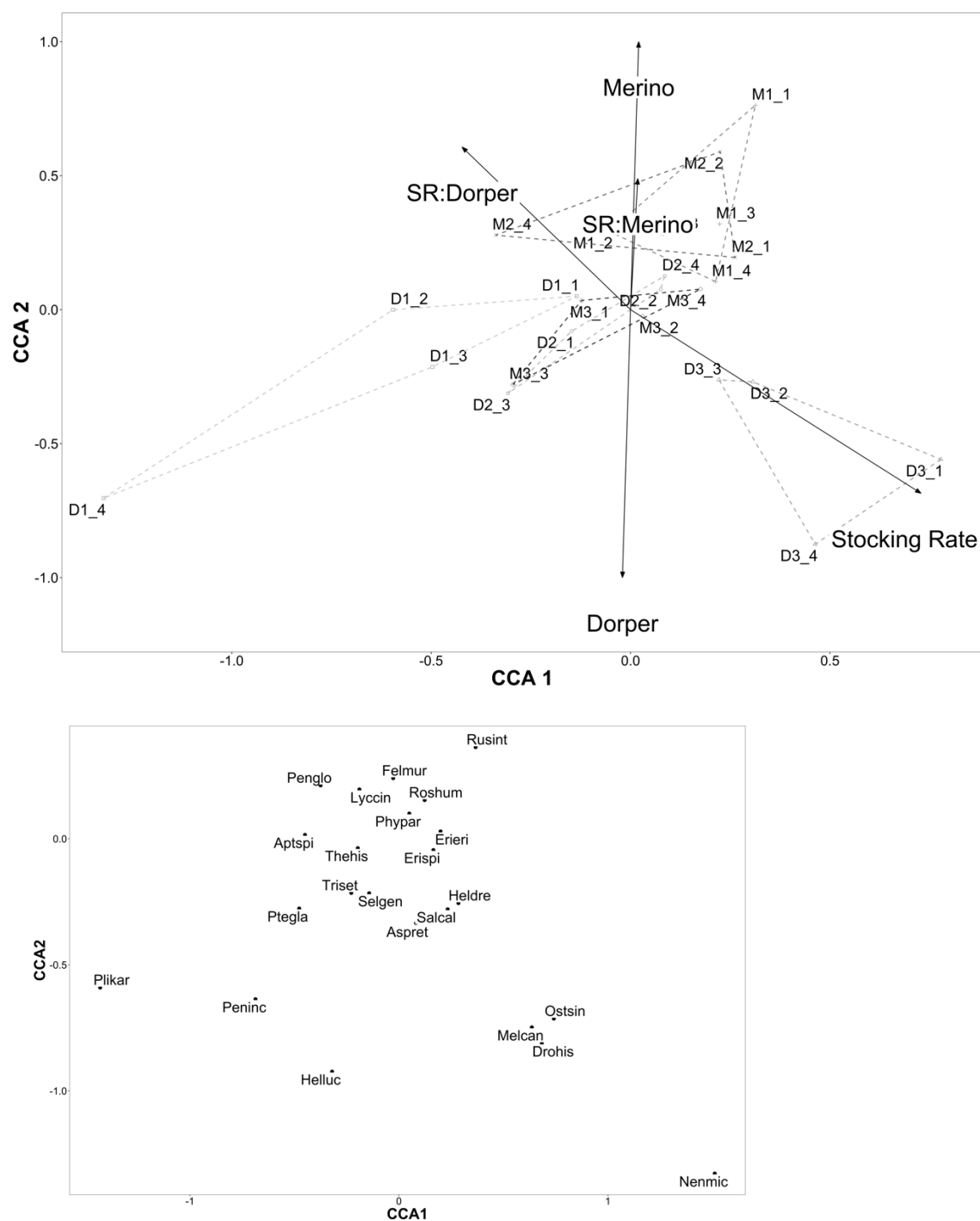


Figure 4: Canonical Correspondence analysis of vegetation composition and species distribution, using average shrub canopy cover in each stratum (one quarter section of each treatment) within each treatment at the Hereford site of the Afrikaner-Hereford grazing trial. Points are labelled according to the trial, livestock breed, stocking rate and stratum number e.g. D1_1 =dorper sheep stocked at 1 ha/SSU, stratum 1.

Shrub community structure

Afrikaner site

There was no effect of animal type on average shrub canopy cover. Stocking rate significantly affected the cover of Karoo shrubs (Table 3, Figure 5). Shrub cover in the intermediate and low SR treatments was significantly higher than in the high SR treatment (Figure 5). The effect of stocking rate on shrub density depended on animal type, for merino sheep shrub density was significantly higher in the low SR treatment compared to the intermediate and heavy SR treatments (Figure 5). For Dorper sheep there was no significant difference in shrub density between low and intermediate SR treatments and shrub density in the high SR was significantly lower than in the low and intermediate SR treatments.

The covariate soil depth significantly affected shrub density where shrubs growing in areas with deeper soils were found in higher densities than those growing in camps with shallower soils.

Stocking rate had a significant effect on the density and cover of palatable shrubs which were both lower in the high SR treatment compared to the intermediate and low SR treatments (Figure 6). Animal type had no significant effect on the density of palatable shrubs but did affect the cover of palatable shrubs which was significantly lower in the high SR treatment compared to the intermediate and low SR treatments (Figure 6). The effect of stocking rate on the density of unpalatable shrubs depended on animal type (Figure 6), with unpalatable shrub density higher in intermediate and low SR treatments, particularly so for merino treatments.

The cover of two functional types; unpalatable dwarf shrubs and palatable dwarf shrubs, were influenced by animal type and stocking rate treatments. There was a significant interaction effect between stocking rate and animal type for average shrub cover of palatable dwarf shrubs. Average cover of palatable dwarf shrubs was higher in intermediate and low SR treatments when grazed with merino sheep compared to treatments grazed with dorper sheep. The average canopy cover of unpalatable dwarf shrubs was significantly affected by animal type and lower in the high SR treatment grazed by dorper sheep compared to the high SR treatment grazed by merino sheep.

The palatable dwarf shrub *Eriocephalus ericoides* had high canopy cover in intermediate SR treatment but had negligible average canopy cover in the high SR treatment (Table 3). The covariate soil depth significantly affected the cover of *Eriocephalus ericoides* which had a

higher average canopy cover in treatments with deeper soils. *Pteronia tricephala*, an unpalatable dwarf shrub, was absent in the high SR dorper treatment, had high cover in the high SR merino treatment and was common in the intermediate treatments. *Selago saxatilis*, a palatable species, was not an abundant species despite being found in all treatments except the high SR dorper treatment (Table 3).

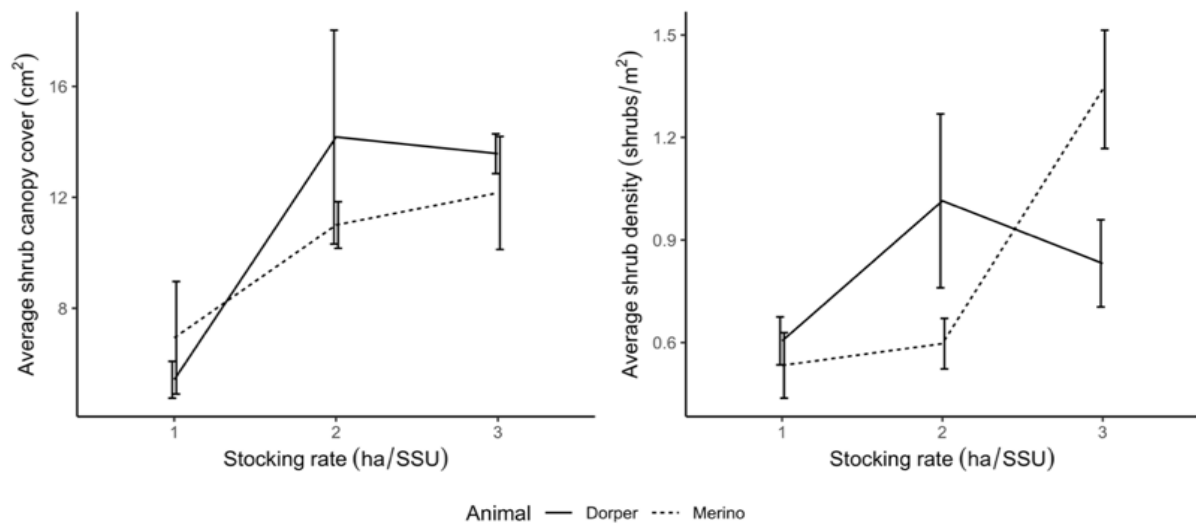


Figure 5: Average canopy cover (cm²) and density (shrubs/m²) $\pm$ SE of shrubs in each stocking rate treatment (hectares per small stock unit) at the Afrikaner site of the Afrikaner-Hereford grazing trial. Dashed lines = merino sheep, black line= dorper sheep.

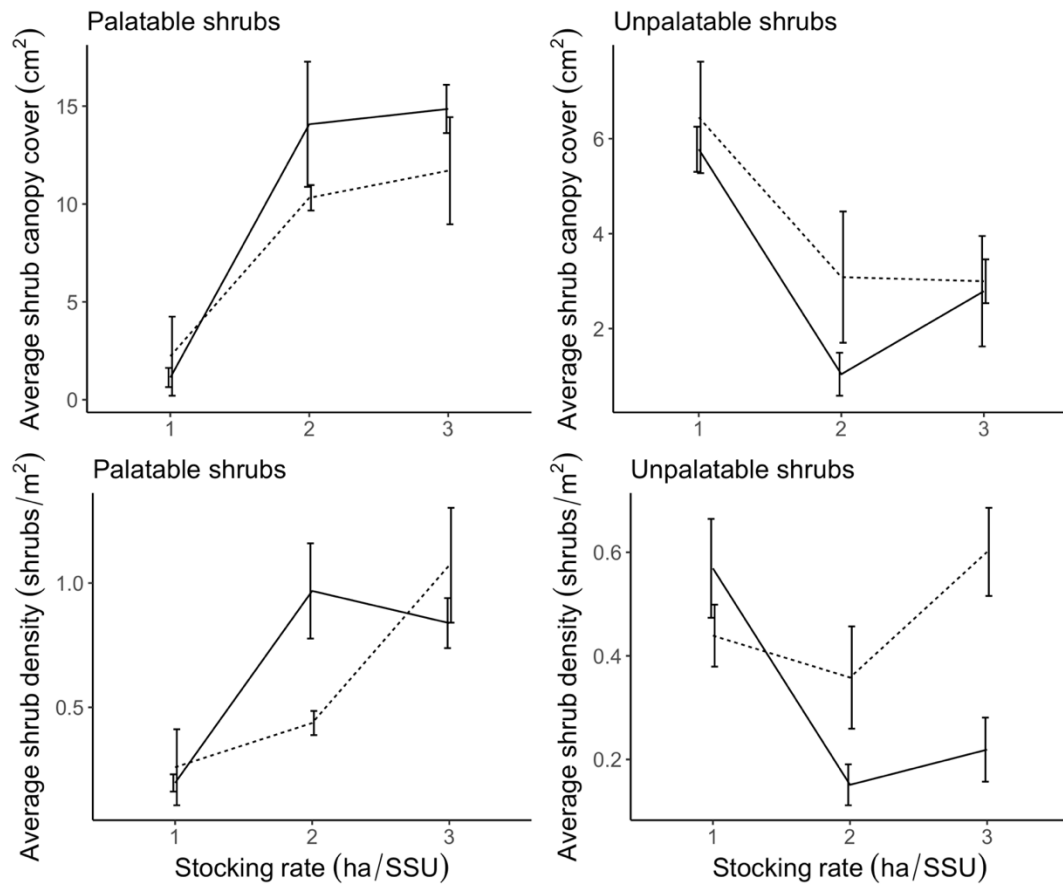


Figure 6: Average canopy (cm²) and density (shrubs/m²) $\pm$ SE of palatable shrubs and unpalatable shrubs in each stocking rate treatment (hectares per small stock unit) at the Afrikaner site of the Afrikaner-Hereford grazing trial. Dashed lines = merino sheep, black line= dorper sheep.

Hereford site.

Average shrub canopy cover and density were both higher at the Hereford site than at the Afrikaner site. Neither average shrub canopy cover nor average shrub density were significantly affected by stocking rate or animal type (Figure 7). Furthermore, there were no significant relationships between stocking rate and animal type for any of the functional types described for the site (Table 4).

A significant interaction between stocking rate and animal type affected the average shrub cover of *Rosenia humilis* which was absent in the high SR treatment grazed by dorper sheep and had its highest cover in camps grazed at a low SR particularly in the merino treatment

(Table 4). The average canopy cover of *Selago geniculata* was significantly higher in intermediate and low SR treatments and in treatments with deeper soils (Table 4).

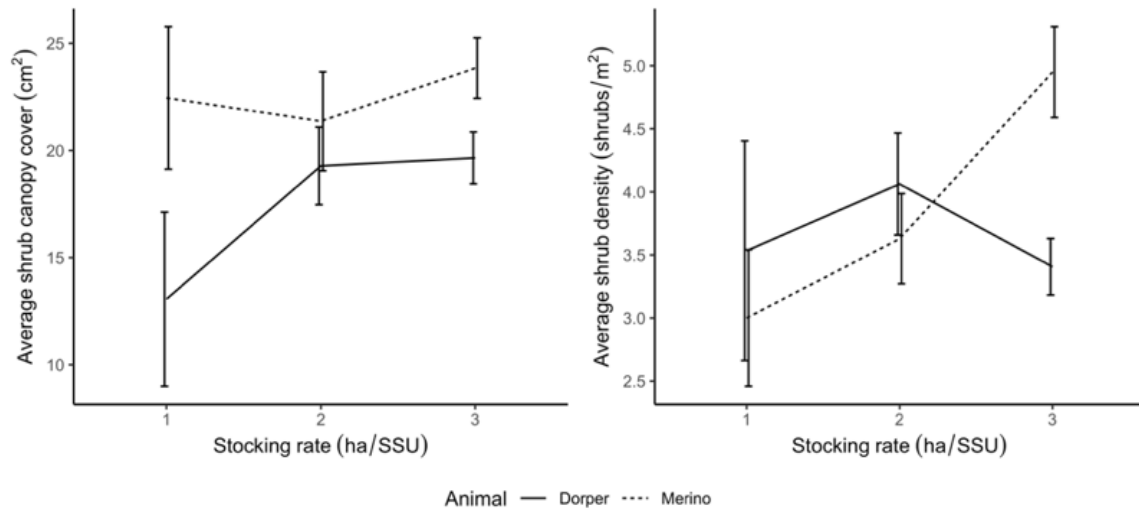


Figure 7: Average canopy (cm²) and density (shrubs/m²) $\pm$ SE of shrubs in each stocking rate treatment (hectares per small stock unit) at the Hereford site of the Afrikaner-Hereford grazing trial. Dashed lines = merino sheep, black line= dorper sheep.

Table 3: Results from an analysis of covariance for average shrub canopy cover (m²) and density (average plants/m²) for all shrubs, functional types and common species at the Afrikaner site of the Afrikaner-Hereford grazing trial ($P \leq 0.05$ presented in bold).

Shrub/Functional type/Species		df	F ratio	P value
Shrub canopy cover	Animal	1,17	0.0103	0.9294
	Stocking rate	1,17	6.685	0.0074
	Animal: Stocking rate	1,17	3.2132	0.0655
	Soil depth (covariate)	1,17	5.4137	0.0325
Shrub density	Animal	1,17	0.0104	0.9198
	Stocking rate	1,17	6.0568	0.0103
	Animal: Stocking rate	1,17	9.4084	0.0018
	Soil depth (covariate)	1,17	5.9536	0.0259
Density of palatable shrubs	Animal	1,17	1.2801	0.2735
	Stocking rate	1,17	6.5055	0.0079
	Animal: Stocking rate	1,17	3.8859	0.4047
	Soil depth (covariate)	1,17	1.1658	0.2953
Cover of palatable shrubs	Animal	1,17	0.4999	0.4891
	Stocking rate	1,17	15.4367	0.0001
	Animal: Stocking rate	1,17	2.6383	0.1004
	Soil depth (covariate)	1,17	3.6256	0.0736
Density of unpalatable shrubs	Animal	1,17	10.0054	0.0057
	Stocking rate	1,17	1.623	0.2264
	Animal: Stocking rate	1,17	5.2477	0.0167
	Soil depth (covariate)	1,17	2.9793	0.1775
Cover of palatable dwarf shrubs	Animal	1,17	0.5624	0.4635
	Stocking rate	1,17	17.2124	<0.0001
	Animal: Stocking rate	1,17	3.5999	0.04971
	Soil depth (covariate)	1,17	1.1658	0.2953
Cover of unpalatable dwarf shrubs	Animal	1,15	7.5724	0.0148
	Stocking rate	1,15	3.3199	0.0640
	Animal: Stocking rate	1,15	3.9926	0.04072
	Soil depth (covariate)	1,17	3.6256	0.0736
Cover of <i>Eriocephalus ericoides</i>	Animal	1,17	0.6153	0.4436
	Stocking rate	1,17	22.3552	<0.0001
	Animal: Stocking rate	1,17	3.7367	0.0452
	Soil depth (covariate)	1,17	6.998	0.0170
Cover of <i>Pteronia tricephala</i>	Animal	1,17	4.6443	0.0451
	Stocking rate	1,17	6.3782	0.0085
	Animal: Stocking rate	1,17	7.6191	0.0043
	Soil depth (covariate)	1,17	0.9315	0.3480
Cover <i>Selago saxatilis</i> (cover)	Animal	1,17	11.413	0.0357
	Stocking rate	1,17	6.6872	0.0072
	Animal: Stocking rate	1,17	0.6457	0.5369
	Soil depth (covariate)	1,17	0.0015	0.9698

Table 4: Results from Analysis of covariance for average shrub canopy cover (m²) and density (average plants/m²) for all shrubs, functional types and common species at the Hereford site of the Afrikaner-Hereford grazing trial ($P \leq 0.05$ presented in bold).

Shrub/Functional type/Species		Df	F ratio	P value
Canopy Cover	Animal	1,17	1.0602	0.3682
	Stocking rate	1,17	5.6794	0.0291
	Animal: Stocking rate	1,17	1.0432	0.3738
	Soil depth (covariate)	1,17	0.0798	0.7810
Shrub Density	Animal	1,17	1.2169	0.3207
	Stocking rate	1,17	0.1150	0.7800
	Animal: Stocking rate	1,17	2.4771	0.1137
	Soil depth (covariate)	1,17	0.5323	0.4756
Cover of Palatable shrubs	Animal	1,17	1.7050	0.2090
	Stocking rate	1,17	0.5361	0.5946
	Animal: Stocking rate	1,17	0.5364	0.5944
	Soil depth (covariate)	1,17	0.50332	0.4877
Density of palatable shrubs	Animal	1,17	0.0343	0.5704
	Stocking rate	1,17	0.5803	0.5104
	Animal: Stocking rate	1,17	1.5926	0.2323
	Soil depth (covariate)	1,17	0.0073	0.9328
Cover of unpalatable shrubs	Animal	1,16	3.2516	0.0902
	Stocking rate	1,16	0.0724	0.9347
	Animal: Stocking rate	1,16	0.7400	0.4927
	Soil depth (covariate)	1,16	0.1553	0.6988
Density of unpalatable shrubs	Animal	1,16	0.9547	0.3431
	Stocking rate	1,16	2.5454	0.1097
	Animal: Stocking rate	1,16	2.0812	0.1573
	Soil depth (covariate)	1,16	3.0863	0.0981
Cover of <i>Rosenia humilis</i>	Animal	1,17	4.5607	0.0476
	Stocking rate	1,17	3.8158	0.0428
	Animal: Stocking rate	1,17	0.8893	0.0426
	Soil depth (covariate)	1,17	4.1756	0.0568
Cover of <i>Selago geniculata</i>	Animal	1,17	0.0233	0.8805
	Stocking rate	1,17	3.6756	0.0471
	Animal: Stocking rate	1,17	2.5358	0.1087
	Soil depth (covariate)	1,17	3.7743	0.0688

Species populations

We did not observe a reverse-J structure for shrub populations as is expected from growing populations which have a dominant state made up of smaller individuals. The dominant state of Karoo shrubs in the Afrikaner-Hereford trial was almost always constituted by mid-size individuals. This indicates that there was little ongoing recruitment in populations of common shrubs at the trial. Patterns in plant height at the trial were not consistent for species within treatments with many species exhibiting different multi-state structures (Table 5). The best fit was a single state for four populations, two-states for 16 populations, and three states for eight populations. A greater number of states than was indicated by the AIC was ecologically appropriate for 12 populations (Table 5).

Eriocephalus ericoides was the most abundant shrub at the Afrikaner site and the only species which occurred in all treatments (Figure 8). The smallest individuals comprised the dominant state for *Eriocephalus ericoides* in the intermediate and low SR dorper treatments but the population in the low SR dorper treatment was comprised of individuals smaller than 10 cm suggesting that this is the only population where larger individuals have successfully recruited. Similarly, in the low SR merino sheep treatment, the proportion of state 1 and state 2 individuals are very similar with the majority of individuals in the smallest and largest stages indicating recruitment has taken place.

Mixture models conducted on plant height for the eleven most abundant species at the Hereford site show species specific responses to historical grazing pressure and animal type (Table 5, Figure 9). Despite many populations having a dominant state of smaller individuals, very small individuals (<10cm) were well represented in only four populations of shrubs at Hereford: *Pentzia globosa* in the high SR of merino treatment, *Phymaspermum parviflorum* in the Intermediate SR merino treatment, and *Trichodiadema setiflorum* in the high and low SR merino treatments. All populations with very small individuals were in high SR and intermediate SR treatments grazed by merino sheep indicating that recruitment took place in those camps but there was little successful recruitment in any of the dorper treatments.

Eriocephalus spinescens populations in treatments grazed by dorper sheep at the Hereford site have populations dominated by intermediately sized individuals indicating no strong evidence of recruitment in the population. The population in the high SR merino treatment had three stages. Stage 1 is made up of individuals smaller than the overall population mean

height indicating a historical recruitment event has taken place. The dominant state of palatable *Pentzia globosa* in high SR dorper and merino treatments is constituted of tall individuals indicating failed recruitment in that treatment whereas populations in intermediate SR dorper and merino treatments and low SR merino treatment have a dominant state made up of small individuals indicative of recruitment having taken place.

The dominant state of the palatable shrub *Phymaspermum parviflorum* in the intermediate SR dorper treatment was composed of small individuals indicating recruitment has taken place in that population. In the low SR dorper treatment the dominant state was composed of intermediately sized individuals, the mean size of these individuals is similar to those in the dominant state of the population in the low SR dorper treatment which had a third state constituted by much smaller individuals suggesting successful recruitment has taken place in that treatment. The high SR merino treatment had only one state while intermediate and low SR merino treatments had populations with three states including a state dominated by small individuals which was absent in the high SR treatments. The dominant state in intermediate and low SR merino treatments was composed of taller individuals (Table 5).

The mean plant height of palatable shrub *Selago geniculata* populations in different treatments at the Hereford site were very similar. Intermediate SR dorper and merino treatments were made up of two states similar in size. A single state made up of small individuals in the low SR merino treatment is indicative of a recruiting population (Table 5). The palatable shrub *Trichodiadema setiflorum* is usually small in stature and grows beneath and between woody stubs. There is only one state in high SR dorper and intermediate SR merino treatments. In the intermediate SR dorper treatment the dominant state is composed of taller plants, a similar pattern was observed in the low SR merino treatment.

There were two species that showed interesting patterns but small sample size limited statistical analysis. *Senecio* sp. was common in the high SR dorper treatment at the Afrikaner site but absent in all other treatments in the trial. *Ruschia intricata* was absent in all dorper treatments but had healthy populations in the merino treatments at the Hereford site.

Table 5: Summary statistics of mixture models and size structure of common species in the Afrikaner-Hereford grazing trial. (SR = stocking rate as hectares per small stock unit, AIC = Akaike's Information Criterion)

Trial	Species	Animal	SR	n	Stages By AIC	Chosen stages	Proportion of plants in			mean height (cm)	Mean height (cm) of plants in		
							state 1	state 2	state 3		state 1	state 2	state 3
Afrikaner	<i>Eriocephalus ericoides</i>	Dorper	2	213	1	2	0.641	0.395		43	37	63	
		Dorper	3	133	1	3	0.112	0.208	0.461	41	52	70	23
		Merino	2	94	1	2	0.852	0.148		42	52	20	
		Merino	3	185	3	3	0.241	0.490	0.268	39	29	68	47
Hereford	<i>Eriocephalus spinescens</i>	Dorper	1	28	2	2	0.895	0.104		21	22	26	
		Dorper	2	31	1	1	1			15	29		
		Dorper	3	44	2	2	0.816	0.183		25	34	24	
		Merino	1	42	3	3	0.251	0.545	0.203	26	18	36	27
	<i>Pentzia globosa</i>	Merino	2	33	2	2	0.488	0.512		20	34	25	
		Dorper	1	47	1	2	0.372	0.627		22	18	28	
		Dorper	2	32	1	2	0.721	0.279		24	23	32	
		Merino	1	32	1	2	0.434	0.556		27	24	32	
	<i>Phymaspermum parviflorum</i>	Merino	2	37	1	2	0.663	0.337		25	23	32	
		Merino	3	44	1	2	0.252	0.748		25	37	24	
		Dorper	2	29	1	2	0.732	0.268		21	26	16	
		Dorper	3	27	3	3	0.179	0.694	0.126	22	40	23	13
	<i>Selago geniculata</i>	Merino	1	25	1	1	1			24	26		
		Merino	2	45	3	3	0.111	0.349	0.54	21	23	15	31
		Merino	3	43	3	3	0.119	0.093	0.787	21	15	22	32
		Dorper	2	38	1	3	0.576	0.172	0.251	23	23	16	32
	<i>Trichodiadema setuliferum</i>	Merino	2	22	1	3	0.184	0.522	0.294	23	34	25	16
		Merino	3	36	2	2	0.972	0.027		21	28	20	
		Dorper	1	40	1	2	1			17	18		
		Dorper	2	25	1	2	0.559	0.44		18	15	26	
		Dorper	3	39	1	2	0.572	0.428		16	20	14	
		Merino	1	22	2	2	0.77	0.227		19	29.2	16	
		Merino	2	20	1	1	1			18	19		
		Merino	3	45	3	2	0.36	0.639		15	22	14	

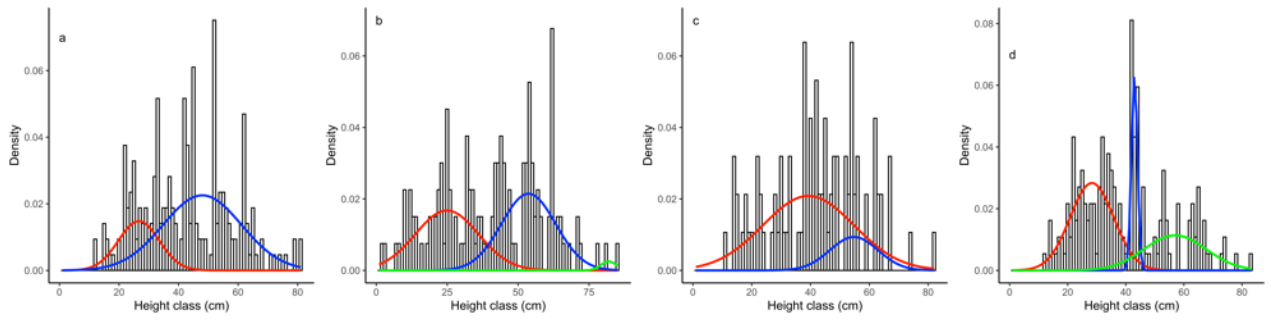


Figure 8: Fitted mixture models using a Weibull distribution for *Erioccephalus ericoides* in a) intermediate dorper, b) low dorper, c) intermediate merino and d) low merino at the Afrikaner grazing trial. States are colour coded as red for state 1, blue for state 2 and green for state 3, refer to Table 5 for the proportion of the total population each state comprises. The number of states fitted using Akaike's Information criterion (AIC); the final number of states chosen was based on ecological criteria (see Methods).

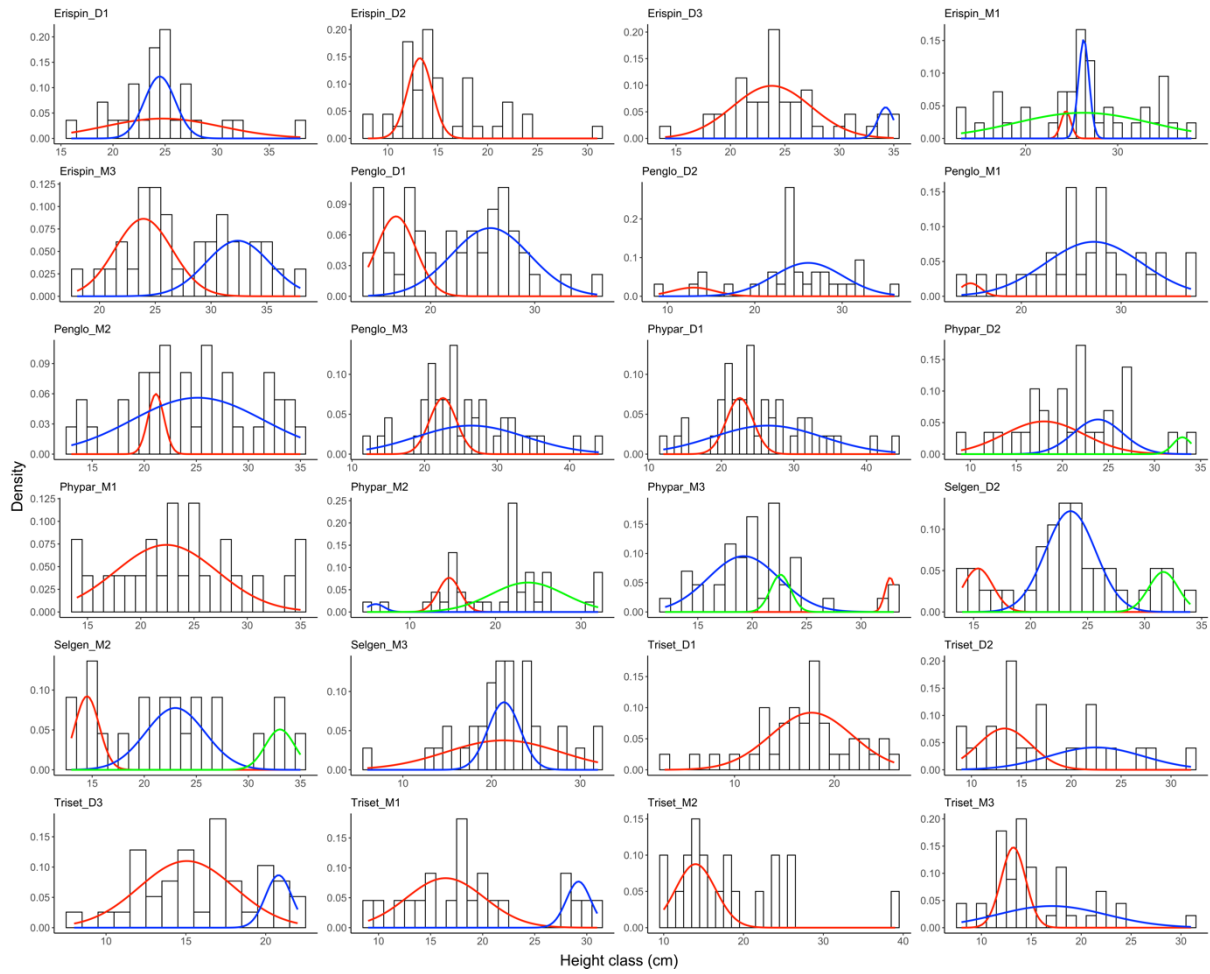


Figure 9: Fitted mixture models using a Weibull distribution for the following species: (a) Erispin= *Eriocephalus spinescens*; Penglob= *Pentzia globosa*; Phypar= *Phymaspermum parviflorum*; Selgen= *Selago geniculata*; Triset= *Trichodiadema setiflorum* at the Hereford site. D1, D2, D3, M1, M2 and M3 indicate animal type (D=dorper and M=merino) and stocking rate, as ha per small stock unit (1 ha/SSU, 2 ha/SSU and 3 ha/SSU). States are colour coded as red for state 1, blue for state 2 and green for state 3, refer to Table 5 for the proportion of the total population each state comprises. The number of states fitted using Akaike's Information criterion (AIC); the final number of states chosen was based on ecological criteria (see Methods).

Discussion

The legacy of grazing management on Karoo shrub communities

Despite ten years of rest and good rainfall preceding this study, the long-lasting effect of grazing by dorper and merino sheep at different stocking rates on shrub community composition of the Afrikaner and Hereford grazing trial sites remained clearly evident. Since good rainfall conditions should have promoted recovery from the effects of the grazing treatments (Figure 1), the differences in composition between treatments can be attributed to grazing as it is unlikely that they have been caused by other successional processes because of the long-lived nature of Karoo shrubs (Milton, 2013). We attribute the changes in shrub communities in the high dorper treatments to the non-selective grazing behaviour of dorper sheep which has a larger impact on individual plants than merino sheep (Brand, 2000). Shrub species that were common throughout the low and intermediate SR treatments at the Afrikaner site, such as *Eriocephalus ericoides* and *Selago geniculata*, were either absent or nearly absent in the high SR dorper treatment indicating they were not able to persist under those conditions. The high abundance of *Senecio* sp. in the high SR dorper treatment at the Afrikaner site is an indication that this species is associated with heavy, less selective grazing by dorper sheep and has replaced more common palatable shrub species.

Ruschia intricata is classified as unpalatable and often becomes the dominant species in communities where it occurs. Communities in which heavy grazing by dorper sheep occurs may result in a drastic change in community composition. The absence of *Ruschia intricata* in all treatments grazed by dorper sheep suggests that this species appears to be particularly sensitive to grazing by dorper sheep despite being classified as unpalatable. This response is similar to that of *Ruschia spinosa* at an overgrazed rangeland in the southern Nama-Karoo where the species did not re-establish in an overgrazed rangeland after 20 years of rest (Seymour et al 2010).

At both trials the presence or absence of specific, usually common species, is an important indication of the degree of change that has taken place at the trial. Such changes demonstrate the legacy of those particular treatments despite the annual and seasonal fluctuations in rainfall which are important determinants of the grazing capacity of Karoo rangelands (Roux and Vorster, 1983). In spite of good growing conditions, the changes in shrub communities in the grazing trial have persisted for ten years. Seymour et al (2010) described changes in a

shrub community over a 20-year rest period. They found that considerable periods of rest, and periods with above average rainfall were still insufficient to allow some shrub assemblages to recover in a Nama-Karoo rangeland. In general, the permanent or semi-permanent compositional changes in Nama-Karoo rangelands can be attributed to the slow turnover of individuals (Esler, 1999). The inconsistent effect of animal type and stocking rate across the two trials suggests that the effects of grazing and stocking rate will vary greatly throughout the Nama-Karoo depending on soil type and shrub community composition.

Soil depth and texture appear to be important determinants of the degree of change driven by stocking rate and animal type in shrub communities at the Afrikaner-Hereford grazing trial. In general plant communities growing on rocky soils are more resilient to disturbance than communities growing in sandy soils (Wonkka et al., 2016). In the Succulent Karoo soil type is an important determinant of community composition and site productivity (Esler and Cowling, 1993). The extent to which this is true is not known for the grassier Eastern Upper Karoo, but it can be assumed that the soil-vegetation relationship is an important determinant for how a rangeland responds to grazing (Esler and Cowling, 1993). The sandy soils at the Afrikaner site support a suite of shrubs which are larger in stature compared to the more diverse community of small statured Karoo shrubs in the shallow rocky soils at the Hereford site.

The interaction between stocking rate and grazing by dorper sheep is more pronounced at the Afrikaner site which has deeper sandier soils. The absence of recruitment at this site is evident in the structure of shrub populations. These results suggest that shrub communities growing in sandy soils are more sensitive to grazing than rocky shallower soils and that communities are changed to a larger extent in deep sandy soils. Furthermore, these communities appear to have a larger legacy affect than those in shallow rocky soils where there is evidence of recruitment for several species at the trial.

The effect of grazing treatment on shrub community structure

As with species composition, the effect of stocking rate and animal type on Karoo shrub canopy cover and density were not consistent across treatments at the Afrikaner-Hereford trial. Vegetation structure contributes to the way in which interactions between individuals takes place within a community. Animal type alone had no impact on shrub community structure but it did interact significantly with stocking rate to have a pronounced negative

effect on the cover and density of palatable dwarf shrubs at the Afrikaner site. High SR treatments had significantly lower shrub cover and density signifying an overall reduction in carrying capacity in those treatments. The high SR dorper treatments resulted in a significant reduction of palatable shrubs and an increase in unpalatable shrubs. The high cover of the common species, *Pteronia tricephala* and *Eriocephalus ericoides* in intermediate and low SR dorper and merino treatments indicates that these two species are sensitive to heavy grazing and can only persist in more leniently grazed systems. Furthermore, they have not re-established in treatments in the ten years since the removal of livestock from the trial illustrating a low rate of recruitment and reestablishment of shrubs at that site and is an indication how the legacy of that grazing treatment remains difficult to measure. The general decrease in palatable species at the Afrikaner site is consistent to what was described by Roux and Vorster (1983), who found that repeated selective grazing degrades a rangeland by depleting the abundance and cover of palatable species.

At the Hereford site only canopy cover was significantly reduced by stocking rate, while the overall density of shrubs as well as the densities of palatable and unpalatable shrubs and of the different functional types did not differ between treatments. At the Hereford site animal type alone had no impact on shrub community structure which appears to be more resilient and is changed to a lesser degree by grazing and high SR than the communities at the Afrikaner site. The common species *Rosenia humilis*, *Pentzia globosa*, *Phymaspermum parviflorum* and *Eriocephalus spinescens*, which were common in the low and intermediate SR treatments, were absent or found in very low numbers in the high dorper SR treatment indicating that these species are sensitive to heavy grazing by dorper sheep. A reduction in cover of common species in a rangeland is important and can indicate a transition to an alternate state (Milton and Hoffman, 1994). A transition to a shrubland dominated by unpalatable shrubs would have long-lasting effects on the carrying capacity of a rangeland. Furthermore, the time required for those palatable shrubs to return to the rangeland is longer than the ten years of rest from grazing the treatment camps at the Afrikaner-Hereford trial received.

Species that appeared to be significantly affected by stocking rate were *Rosenia humilis*, *Eriocephalus ericoides* and *Ruschia intricata*. Similar patterns in canopy cover change have been described (Van der Merwe et al., 2018) which showed that the canopy cover of *Rosenia*

humilis, *Eriocephalus ericoides* and *Ruschia intricata* declined with increasing animal stocking rate.

Species populations in grazing treatments

Mixture models revealed no general patterns of shrub height for populations in the grazing treatments at the Afrikaner-Hereford trial illustrating that individual species responded differently to the same grazing treatment. The dominant state of most populations at the Hereford and Afrikaner sites was dominated by intermediately sized and large individuals. The poor representation of small individuals indicates signs of recruitment-failure in most populations suggesting that under most grazing regimes the majority of common shrub species are not able to recruit successfully with an extended rest period during which good rainfall was received. This may be in part due to the environmental requirements for shrub seeds to persist, germinate and survive in the landscape (Esler, 1999). A study of seed banks in the Tankwa Karoo found large spatial variation in the amount and composition of seeds in seed banks. Nearly half of the seeds collected were those of shrub species and approximately 55% of the seeds were viable (Saeed et al 2018). Henrici (1935) described the high variability of seed production and viability of karoo shrubs and how the germination requirements of species varied greatly under laboratory conditions. The very small number of seedlings or very small individuals indicates that recruitment at the Afrikaner- Hereford grazing trial has not taken place in the ten-year period of rest despite the presence of larger reproductive age shrubs. It is unclear whether the legacy of each grazing regime on older populations of species in the trial has had a long-term effect on shrub recruitment.

Most species were not able to persist in the high SR dorper treatment at the Afrikaner trial, only small populations of a few species remained, and the grazing potential of that treatment was very poor. This effect was not seen at the high SR dorper treatment at the Hereford site illustrating that grazing management alone does not determine the impacts on shrub populations (Seymour et al 2010, du Toit 2014, Hebbelmann et al 2022).

Grazing treatment had a marked effect on the demographic performance of palatable shrubs under high SR treatments which had shorter average heights despite being rested for more than ten years before being measured. Some species which had a large proportion of individuals in a taller stage were generally found in the treatments grazed at intermediate and low stocking rates. Since reproductive success of shrubs is positively related to their size the

reproductive output of smaller individuals is reduced as their cover is reduced (Silvertown and Charlesworth, 2009).

Importance of long-term grazing trials

The changes in shrub community composition and structure at the Afrikaner-Hereford grazing trial demonstrates that grazing is an important determinant of Karoo vegetation composition and structure (du Toit and O'Connor, 2020; Kraaij and Milton, 2006). At the Afrikaner-Hereford trial it appears that animal type is only important at high stocking rates. This may suggest to land managers that high stocking with dorper sheep is potentially damaging to Karoo rangelands and that grazing induced changes can persist for a long time. Annual changes in rangelands are small but as they accumulate over time they become substantial because the direction of change is usually consistent for a given species (O'Connor and Roux, 1995).

The Afrikaner-Hereford grazing trial is one of very few grazing trials which offer long term monitoring of the impacts of animal grazing and stocking rate on Nama-Karoo veld. Our study provides a snapshot of changes that have occurred over a long time clearly demonstrating a legacy effect of grazing intensity and animal type on two Karoo shrub communities. The patterns observed at the trials are consistent with the state-and-transition model for the eastern Nama-Karoo, but we demonstrate that there is a clear legacy effect at the grazing trial meaning that recovery or return to its pre-trial condition may be a very slow process. Communities which have been changed by the grazing treatments do not appear to be returning to mixed rangeland after prolonged rest. Any studies on recruitment will require long term monitoring offered by these trials if we are to better understand the drivers of Nama-Karoo rangelands.

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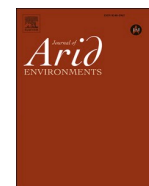
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Fire as a novel disturbance and driver of vegetation change in Nama-Karoo rangelands, South Africa

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ABSTRACT

Nama-Karoo vegetation is fire naïve and therefore vulnerable to transformation by fire. This study investigated the effect of fire, a novel disturbance, on the composition and structure of shrub communities in semi-arid Eastern Upper Karoo rangelands. Nine sites across a rainfall gradient had been burnt between eight years and six months before time of sampling, whose grazing history ranged from heavy or lenient to no grazing. Fire markedly changed the composition and structure of Karoo shrublands, the nature and extent of which depended on climate regime. Non-sprouting species, including some dominant species, were extirpated by fire and replaced by previously non-dominant sprouter species. Replacement of non-sprouter by sprouter species was conspicuous for palatable and unpalatable dwarf shrubs. Under conditions that closely resemble climate change forecasts for the region, fire transformed Nama-karoo shrublands. The possibility of larger more frequent fires in the Nama-Karoo threatens to transform the vegetation, ecosystem functioning, and economy of the region. Fire has emerged as a novel agent of vegetation change in the eastern Nama-Karoo owing to a directional increase in annual rainfall over the past three decades, that may cement a state change from shrubland to grassland in an ampliative, positive feedback manner.

1. Introduction

Fire is an important global driver of vegetation change, the presence or absence of which, in conjunction with climate, can determine the distribution of biomes (Bond and Keeley, 2005; Thonicke et al., 2001). Frequent fires in grassland prevent the establishment of woody species thereby preventing a shift to savanna or forest, but low amounts of flammable biomass results in a low incidence of fire in arid areas (Bond and Keeley, 2005). The characteristics of a fire - intensity, size, and return interval - influence ecosystem functioning and on post-fire recovery of plant communities (He et al., 2019). Different intensities of a disturbance may result in differences in the survival rate of plant populations and patterns of recovery over time (Collins and Barber, 1985). Fire-naïve vegetation communities are likely to experience larger compositional and structural changes compared to those that are fire-prone and accustomed to large disturbance events (Gordijn et al., 2018).

Climatically driven vegetation change has the potential to expose previously fire-naïve communities to fire for the first time. An increase

in flammable species, or of the flammability of vegetation as a result of climate change such as warmer temperatures and lower humidity provide the possibility for novel fire events (Kirchmeier-Young et al., 2019). For example, fire occurred in some shrublands following the invasion of alien grasses (Rahlao et al., 2009), and the frequency of forest and bush-fires in Australia has increased owing to an increase in frequency of very hot, dry and windy periods (Matthews et al., 2012). The extent of the 2018 fires in the Knysna region of South Africa were attributed to drought and exceptional dry hot weather (Kraaij et al., 2018). The Nama-Karoo biome of South Africa is an example of previously fire-naïve vegetation becoming exposed to fire on account of altered climatic patterns.

The semi-arid Nama-Karoo biome occupies the western interior of South Africa (Mucina et al., 2006), and is characterised by a layer of dwarf shrubs interspersed with annual and perennial grasses. The abundance of grass increases along a west-to-east gradient of increasing rainfall to the transition from the Nama-Karoo biome into the Grassland Biome. The eastern Karoo has become increasingly grassy over the past several decades; in effect the Grassland Biome has expanded westwards

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into the Nama-Karoo Biome (Masubelele et al., 2014, 2015), a change attributed to a pattern of increasing rainfall and a reduction in livestock stocking rates over time (Hoffman and Cowling, 1990; Masubelele et al., 2015). Most grass species growing in the Nama-Karoo are C_4 species and are therefore highly responsive to rain during warm summer months.

Climate models predict an increase in summer rainfall for the eastern Karoo (Engelbrecht et al., 2009) and long-term rainfall patterns are consistent with this (du Toit and O'Connor, 2014; Harmse et al., 2021). A trend of increasing rainfall has been recorded for the eastern Nama-Karoo over the past 30 years, with a period of particularly high rainfall between 2010 and 2012 (du Toit and O'Connor, 2014). Subsequent increases in grass biomass resulted in high fuel loads and a number of fires on Karoo plains where they had not previously been recorded (du Toit et al., 2015a). The effect of these fires was to induce a shift from a dwarf shrubland to a sparse grassland because grasses regrew relatively quickly after the fire (du Toit et al., 2015a) and results from a single-site study showed fire-induced change in the plant community may persist (du Toit et al., 2015b). Although fire-tolerant resprouting species were not killed by fire, their regrowth was typically slow. However, populations of fire-intolerant non-sprouting species, often locally dominant, were extirpated by fire resulting in a drastically altered post-fire community (du Toit et al., 2015a; 2015b). The abundance of sprouting and non-sprouting species, therefore plays an important role in post-fire recovery of composition by a community (Archibald et al., 2005). Recovery of fire-intolerant non-sprouter species is severely constrained because they can only re-enter the community from seed (Van Wilgen, 2013), and their recovery is usually constrained further by a limited set of environmental conditions under which regeneration can occur (Wiegand et al., 1995).

The effect of fire on rangelands can rarely be isolated from its association with grazing (Archibald et al., 2005; Fuhlendorf and Engle, 2004). Both affect plant community structure and composition, and the functioning of rangeland ecosystems (Archibald et al., 2005; Bond and Keeley, 2005). Furthermore, grazing management following burning can have a major impact on the stability of rangeland (Everson, 1999) and may influence the rate of vegetation recovery. Current understanding of the response of Nama-Karoo vegetation to rainfall and grazing, based on either empirical study (Hoffman and Cowling, 1990; Masubelele et al., 2014; O'Connor and Roux, 1995), or models (Milton and Hoffman, 1994; Wiegand et al., 1995) has never had to consider the effect of a novel event such as fire. However, such an event, based on similar events globally (fire, floods and landslides), is expected to result in a dramatic and long-lasting reorganisation of the shrub community (Kulakowski et al., 2006).

The Nama-Karoo is an economically important livestock farming region, for which the implications of vegetation change for sustainable rangeland and livestock management need to be understood. Shrubs provide year-round forage for livestock and are especially important during the dry, cold winters when grass biomass is low. Grasses are advantaged by periods of high summer rainfall and provide the bulk of forage during the summer (O'Connor and Roux, 1995; Roux and Vorster, 1983). If rainfall-driven grass cover increases, it may result in increased competition by grasses causing a reduction in shrub abundance (Hoffman and Cowling, 1990) and, thereby, reduced forage availability during winter. Ultimately, this would affect livestock production. However, the introduction of fire is expected to have a far greater impact on shrubs than competition from grasses would. Understanding the response of Nama-Karoo vegetation to fire is therefore important because it is likely to have consequences for agriculture, natural resources and biodiversity.

Opportunities to explore the effects of fire as a novel disturbance in semi-arid environments are rare, particularly under changing climatic conditions that represent conditions predicted under climate change (MacKellar et al., 2014). The period of high rainfall preceding the fires discussed in this study closely resemble climate predictions by Engelbrecht et al. (2009), which predict a significant increase in mean annual

rainfall for parts of the Eastern Upper Karoo. This was the first multiple-site study undertaken to understand the effect of fire on Nama-Karoo shrublands on plains over a large geographic area and rainfall gradient, and under different grazing pressures. We first sought to establish the extent to which the composition and structure of shrub communities on Nama-Karoo plains were affected by fire across an east-to-west rainfall gradient. We then sought to determine the extent to which a single fire might transform fire-naïve vegetation, and to identify which vegetation components were particularly susceptible. It was expected that: (i) shrub community composition and the composition of different functional types would change; (ii) fire-intolerant species might become locally extirpated by fire; (iii) following a fire, shrub density, cover and height would decline but recover with time depending on the amount of rainfall received; and (iv) shrub recovery after a fire depends on herbivory, with shrub cover, density and height not expected to recover to the same degree on heavily grazed rangeland as they might on lightly grazed rangeland.

2. Materials and methods

2.1. Study area and fire sites

This study was conducted at nine fire sites in the Eastern Upper Karoo (Mucina et al., 2006), a region characterised by flat plains interspersed with rocky hills (Table 1). Mean annual rainfall ranged from 288 mm to 372 mm along a gradient from southwest to northeast. Inter-annual variation in rainfall is high; for example, annual rainfall at Middelburg measured over 123 years has fluctuated between 118 and 731 mm (du Toit and O'Connor, 2014). Rainfall over the past 30 years has been higher than it was during the preceding 80 years. Rainfall seasonality is slightly variable, but the majority of rain falls during summer. Summer rainfall in the years preceding the fires in this study was high, favouring grass growth (du Toit and O'Connor, 2014). During mid-summer (November to February), daily maximum and minimum temperatures range between 23 °C and 30 °C, and 10 °C and 16 °C, respectively. During mid-winter (June to August), maximum and minimum temperatures range between 10 °C and 16 °C and −4 °C and 4 °C, respectively, but regularly drop below −5 °C, with an average of 62 frost nights per year at Middelburg (du Toit and O'Connor, 2016). Grasses are cured by these frosts each year in early winter. Soils are generally shallow, weakly developed, lime-rich and sandy, and overlie sediments of the Beaufort Group Formation (Mucina et al., 2006). Vegetation is classified as Eastern Upper Karoo (Mucina et al., 2006) and is shrubland dominated by microphyllous Karoo dwarf shrubs interspersed with grasses mainly of the *Eragrostis* and *Aristida* genera. The northeast area of the Eastern Upper Karoo is an ecotone between the Nama-Karoo and Grassland Biomes.

Commercial livestock ranching is the primary economic activity in the Nama-Karoo, based mainly on sheep and cattle stocked at 12–25 ha per large stock unit (Meissner et al., 1983). Commercial rangelands are generally stocked at low stocking rates and rangelands are rested periodically. Communal farming areas are grazed continuously at high stocking rates and are therefore usually in poor condition (Hoffman and Todd, 1997).

This study located nine fire sites. Six had burnt during the wet period between 2010 and 2012 (du Toit and O'Connor, 2016), and three had burnt in 2017 (Table 1). Sites were chosen according to accessibility, that they burnt on plains and not mountains, and that the boundary between burnt and unburnt fractions was clear. The extent of each burn was contained by land owners or local communities.

Sites were distinctly different in vegetation owing to an increasing gradient in rainfall from west to east. The western sites had the lowest grass cover and were dominated by the shrubs *Pentzia globosa*, *Eriocephalus ericoides*, *Ruschia intricata* and *Selago* species. (Plant nomenclature follows SANBI (2019)). Sites in the central region supported an intermediate grass cover and were dominated by the shrubs *Eriocephalus*

Table 1
Description of the nine locations at which fire was studied in the eastern Nama-Karoo.

Fire site and code	Coordinates	Year of burn	Burnt area (ha)	Land use	Grazing pressure (since burn)	MAR (mm) at nearest measured location.	Region	Soil texture (Clay %)
Victoria West Commonage (VW)	31.4206° S 23.1641° E	2011	1500	Communal Rangeland	Heavy	288	Victoria West	21
Inverness Farm (IF)	31.3797° S 22.9172° E	2012	1450	Commercial farm	Lenient	288	Victoria West	20
Richmond Siding (RS)	31.3673° S 24.0282° E	2010	180	Road reserve	Rested	330	Hanover	17
The Mills Farm (TM)	31.1749° S 24.3727° E	2011	1000	Commercial farm	Lenient	313	Hanover	19
Middelburg Commonage (MC)	31.5219° S 24.9834° E	2010–2012	44	Communal rangeland	Heavy	361	Middelburg	14
Boesmanskop Grootfontein (BK)	31.4355° S 25.0250° E	2012	24	Research farm	Lenient, Rested	372	Middelburg	3
Helpmekaar Farm (HF)	31.4906 S 25.1816 E	2017	600	Commercial farm	Rested	372	Middelburg	15
Redlands Farm (RF)	31.4814 S 25.3144 E	2017	16	Commercial farm	None	372	Middelburg	12
Brienne Farm (BF)	31.4416 S 25.5164 E	2017	8	Commercial farm	Lenient	353	Middelburg	15

spinescens, *Pentzia globosa*, *Phymaspermum parvifolium* and *Delosperma multiflorum*. Sites in the eastern region had the highest grass cover and the dominant shrub species were *Eriocephalus ericoides*, *Eriocephalus spinescens*, *Pentzia incana*, *Chrysochroma ciliata* and *Felicia muricata*.

2.2. Field surveys

The sampling approach was modelled on the ‘fence-line’ contrast approach used in landscape-level grazing studies (Noy-Meir et al., 1989). This was possible because individual fires had created clear, sharp boundaries between burnt and unburnt vegetation, and the position of the boundary was determined by the prevailing wind and not by vegetation characteristics. At each site, paired plots were sampled either side of a fire boundary, ensuring that a pair of plots did not differ in terms of land management, topography, or edaphic properties. The number of, and spacing between, paired plots depended on the length of the fire boundary at each site. A minimum of five paired plots and maximum of fifteen paired plots were sampled per site. Paired plots were spaced between 20 m and 50 m apart, 20 m on either side of the burn boundary. Anomalous patches such as gulleys, river beds or other large bare areas were excluded. Surface soil was collected to a depth of 10 cm in three plots at each site using a soil auger. Site samples were pooled and tested at the Soil Fertility and Analytical Services Section of the KwaZulu-Natal Department of Agriculture and Rural Development at Cedara in Kwa Zulu Natal, South Africa. Soil physical properties of sand and clay percentages were measured using procedures described by Manson et al. (2000).

Vegetation was sampled using circular plots, with a plot radius of 2 m at sites where Karoo shrubs were sparse, and 1 m at other sites. Large plots accommodated approximately the same number of plants and species as small plots. All shrubs within a sample plot were identified and enumerated. Multi-stemmed plants were defined by the aggregation of their stems or visible vegetative anchoring common in some Karoo dwarf shrub species (Esler, 1999). Shrub height, the longest canopy diameter (2r) and the canopy diameter perpendicular to this (2q) were measured, and the proportion (L) of the canopy bearing growing leaves was estimated. Plant canopy area (A) was defined as the area of the shrub with actively growing leaves, and calculated as $A = (\pi r q) L$.

Plant functional types were defined based on growth form, plant height, leaf succulence, parasitism and grazing index values (GIV). Grazing index values are allocated to each species according to their capacity to produce fodder for livestock, seasonal nutritional quality, ease with which livestock can forage on a plant, life history strategy, and the capacity of an individual plant to protect the soil (Botha et al., 2001). Karoo shrubs with a GIV <4.25 were classified as unpalatable and all

shrubs with a GIV ≥ 4.25 were classified as palatable. Dwarf shrubs characterise Karoo shrublands and their low stature (<50 cm in height) and twisted woody stems distinguish them from other shrub species. The following functional types were recognised: Palatable dwarf shrub <30 cm in height, Palatable dwarf shrub >30 cm in height, Palatable leaf succulent dwarf shrub, Unpalatable Dwarf shrub <30 cm in height, Unpalatable dwarf shrub >30 cm in height, Unpalatable parasitic dwarf shrub, and shrubs (generally growing to >1 m, not dwarf species).

2.3. Data analysis

Community composition was examined using Canonical Correspondence Analysis (CCA), a direct gradient analysis technique, which allows for explicit testing of the effect of the environmental variables of *a priori* interest. Sample size was small due to the rarity of fire in the Karoo, and the nine sites encompassed a wide range in management history that was assumed to have had a site-specific effect on community composition. We therefore adopted a two-stage approach to the community analysis. First, an analysis of composition across all sites with fire and rainfall as environmental variables, and, second, an analysis of each individual site with only fire as an environmental variable, were undertaken. CCA was undertaken using the Vegan package in RStudio (Allaire, 2016; Oksanen et al., 2015).

Scaling was focused on inter-sample differences using biplot scaling. Average canopy cover per species was the measure of abundance used. Species with five or fewer observations were excluded. A Monte Carlo test (999 permutations) was used to test the significance of the first axis and of the ordination overall. The effect of fire on community composition was tested for significance.

A Bray-Curtis dissimilarity measure was calculated using species cover data for each pair of burnt and unburnt plots, using the Vegdist function in the Vegan package in RStudio (Allaire, 2016; Oksanen et al., 2015). A linear regression was used to examine the effect of rainfall and the time since fire (age) on the dissimilarity of paired burnt and unburnt plots across the nine fire sites (separate regressions were required on account of a low sample size). The effect of fire on the shrub canopy cover of each plant functional type was analysed using paired t-tests, including only old burn sites in which shrubs had had an opportunity to regrow since the fire had occurred.

The effects of fire, rainfall, time since burn, and grazing pressure on the average height, density and canopy cover of shrubs at the nine sites were investigated using a general linear model (GLM) (Allaire, 2016). Since time since burn and post-fire grazing pressure can have cumulative effects, their interactions with fire were included in the analyses, but removed if found to be non-significant. Shrub height, density and

canopy cover data were. A paired *t*-test (Allaire, 2016) was used to compare shrub height, density and cover between burnt and unburnt plots at each site, after testing each for normality and transforming if necessary. The proportional cover of non-sprouting and sprouting shrubs in burnt and unburnt plots across all sites was compared using *t* tests.

3. Results

3.1. Vegetation composition

Ordination successfully identified a conspicuous effect of rainfall and fire on shrub composition (Fig. 1). Compositional differences between burnt and unburnt rangeland were greater at high rainfall than at low rainfall sites (Table S.1).

Site-specific ordinations showed that burnt and unburnt plots supported a significantly different ($P < 0.05$) shrub composition for Inverness Farm, Richmond Siding, The Mills Farm, Middelburg Commonage, Redlands Farm, Boesmankop, and Helpmekaar Farm, a marginally significantly different ($0.10 > P > 0.05$) composition for Brienne Farm, only a year after the fire, and there was no difference on the Victoria West commonage (Fig. 2, Table S.1). For the last-mentioned site, grazing pressure was very high and species richness was very low, with both burnt and unburnt sites dominated by resprouting species, predominantly *Pentzia globosa* (palatable), *Rosenia humilis* and *Pteronia tricephala* (both unpalatable). Conspicuous patterns across the eight sites showing a compositional difference between burnt and unburnt portions was the abundance of fire-intolerant species on unburnt sites but their absence or poor representation on burnt sites, the apparent benefit to some species through creating an opportunity for recruitment, and dominant resprouter species usually maintained their dominance following fire although their abundance may decrease.

In respect of fire-intolerant species, *Ruschia intricata* and *Eriocephalus ericoides* were abundant in unburnt plots (21% and 17% respectively) but were absent in burnt plots, as were the rare *Salsola aphylla*, *Drosanthemum hispidum* and *Sarcocaulon samoensis* at Inverness Farm. At the Richmond Siding, some recruitment of the fire-intolerant species *E. ericoides* (17% in unburnt, 10% in burnt) and *Delosperma multiflorum*

(19% in unburnt, 5% in burnt) appeared to have occurred following fire, but not for *Helichrysum lycioides* or *Pteronia glauca* (6–7% on unburnt, absent on burnt). At the Mills Farm, *E. ericoides*, *Felicia muricata*, *Eriocephalus spinescens*, *Selago saxatilis* and *Selago geniculata* were found in unburnt plots but were absent in burnt plots. On the Middelburg commonage, *E. spinescens* and *R. intricata* were moderately abundant in the unburnt plots (~9%) but were absent in burnt plots, and nine uncommon species found in unburnt plots were absent in burnt plots. The most abundant species in unburnt plots on Redlands Farm, namely *E. ericoides*, *E. spinescens* and *S. saxatilis* (8–10%), were absent in burnt plots. At Boesmankop, *E. ericoides* was found in unburnt (9%) but not burnt sites. At Helpmekaar, *E. ericoides* and *Chrysochroma ciliata* were abundant in unburnt plots (25% and 29% respectively) but were absent in burnt plots. At Brienne Farm, *E. spinescens* was relatively common in unburnt plots (18%) but absent in burnt plots.

Species whose abundance apparently increased following a fire were abundant on burnt plots but absent or poorly represented on unburnt plots, indicating that fire may have encouraged establishment of these species. Examples included *Melolobium candicans* (20%, 0%) at Richmond Siding, *Helichrysum zeyheri* (10%, 0%) at Boesmankop, *Selago geniculata* (44%, 7%) at Helpmekaar, and *Thesium hystrix* (28%, 0%) and *Nenax microphylla* (11%, 0%) at Brienne Farm.

Sites at which resprouter species were dominant and had their abundance reduced by fire but usually remained a dominant species included only *Pentzia globosa* (43%, 33%) at Inverness Farm, the Mills Farm (61%, 11.8%), and at the Richmond Siding (29%, 18%). By contrast, dominant resprouter species less affected by fire included *Pteronia tricephala* (11% in burnt, 20% in unburnt) at Mills Farm, *Pentzia incana* (26% in burnt, 17% in unburnt) on Middelburg Commonage, a palatable species that has the ability to survive heavy grazing owing to its growth form, *Felicia muricata* (10% in burnt, 21% in unburnt) at Boesmankop, and *Lycium cinereum* (34% in burnt, 39% in unburnt) at Brienne Farm, which is a shrub, not a dwarf shrub species that may be locally dominant. New burns had much fewer species in burnt areas, ostensibly because some species had not yet begun resprouting.

3.2. Shrub compositional change

There was a significant linear relationship between mean annual rainfall (MAR) and compositional dissimilarity between burnt and unburnt sites ($\text{Dissimilarity} = -0.749 + 0.004 \text{ MAR}$ ($F_{1,7} = 7.818$, $P = 0.027$, $R^2 = 0.46$, Fig. 3). Burnt and unburnt plots at high rainfall sites are more dissimilar than those in the drier western sites. Compositional dissimilarity between burnt and unburnt plots of each site was linearly related to the time since fire (years) ($\text{Dissimilarity} = 0.846 - 0.054 \text{ Years}$ ($F_{1,7} = 13.48$, $P = 0.008$, $R^2 = 0.61$, Fig. 3). Compositional dissimilarity between burnt and unburnt sites at recently burnt sites (Redlands farm, Helpmekaar farm and Brienne farm) was higher (82%) than at older burn sites (51%), indicating that rangeland tended towards its pre-burn composition over time.

3.3. Shrub community structure

A general linear model for all sites showed that shrub height, canopy cover and density were not affected by fire, grazing pressure, years since fire or rainfall, nor by any interaction among these variables (Table S.2) and there was no significant difference in shrub community structure between burnt and unburnt plots. When each site was analysed separately the effect of fire on shrub community structure was significant at only three of the nine sites (Table 2). Shrub canopy cover was significantly lower in burnt areas at Inverness farm ($t = -2.134$, $df = 15$, $P = 0.050$) and at Helpmekaar farm ($t = -3.545$, $df = 7$, $P = 0.009$). At Boesmanskop, shrub density was significantly lower in burnt plots compared to unburnt plots ($t = -2.362$, $df = 12$, $P = 0.036$) owing to the high proportion of non-sprouters which were eliminated in the fire.

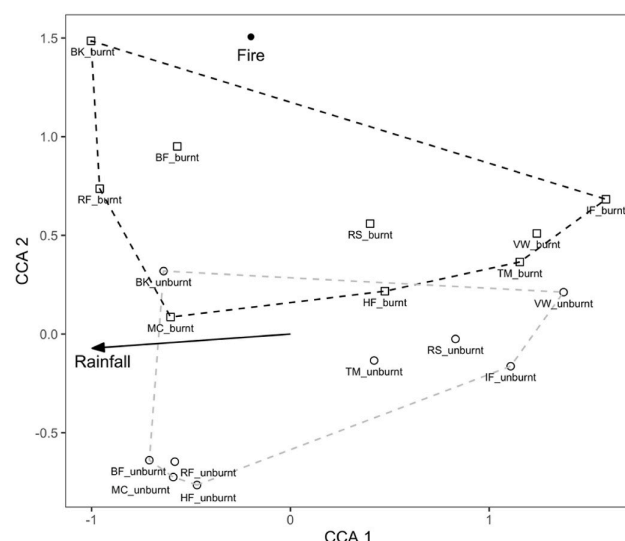


Fig. 1. Canonical Correspondence analysis (CCA) for all sites showing sites grouped according to burn. (Burnt areas = black envelope, unburnt areas = grey envelope, burnt plots = open squares, unburnt plots = open circles; see Table 1 for site codes). Eigenvalues (percent of variance): axis 1 = 0.5731 (15.6%); axis 2 = 0.2924 (7.7%). Fit of environmental factors: Rainfall, $P = 0.001$; Fire, $P = 0.026$.

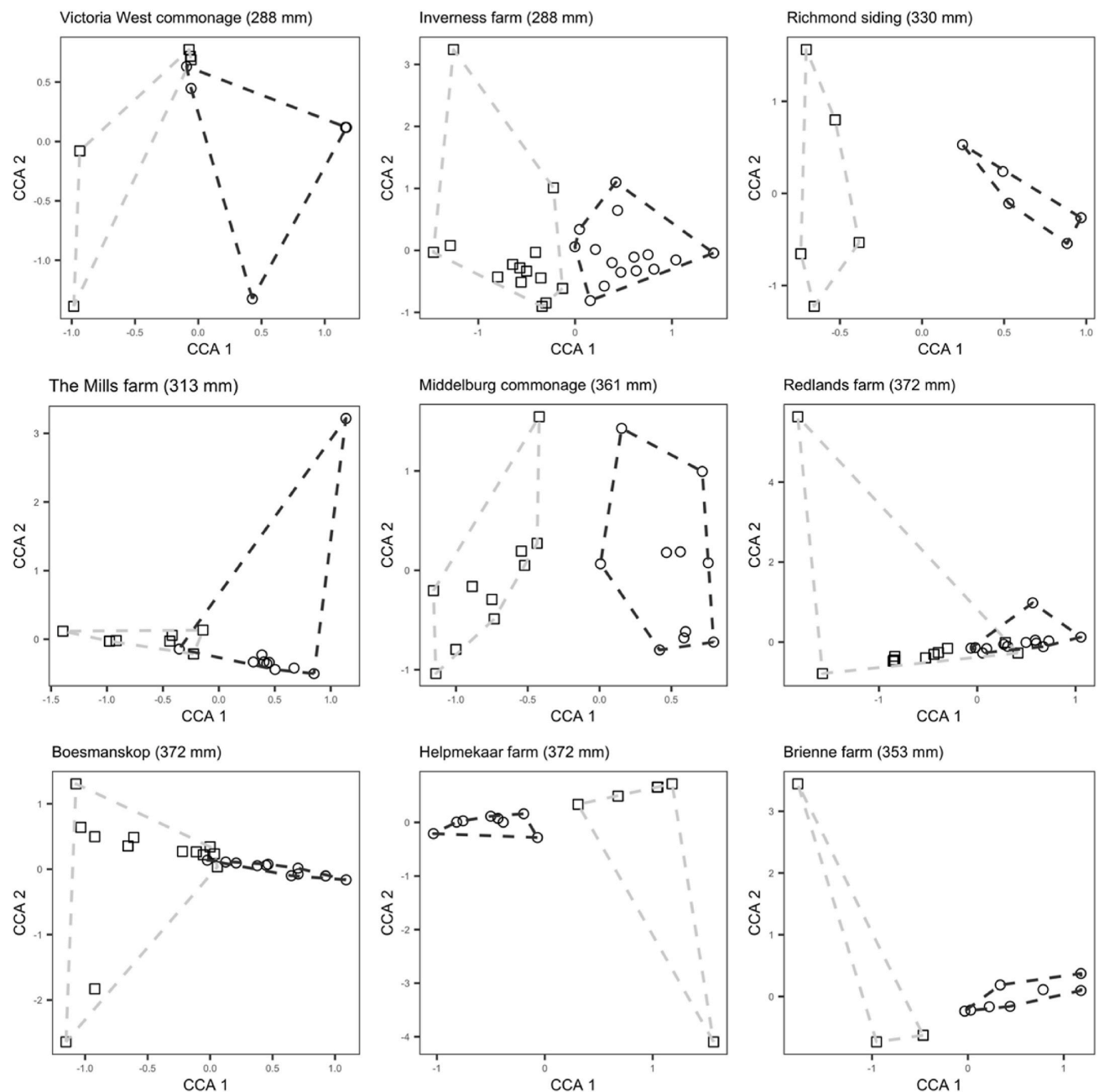


Fig. 2. Canonical Correspondence analysis (CCA) for each site showing sample plots grouped according to burn. (Burnt areas = black envelope, unburnt areas = grey envelope, burnt plots = open circles, unburnt plots = open squares).

3.4. Presence of non-sprouter and resprouter shrubs

Thirteen non-sprouter species were identified that were present in six of the nine functional types (Table S.3). Non-sprouter species were measured in all nine of the unburnt areas and seven of the nine burnt sites, at which they were present in very low numbers. These individuals were either immature plants or had escaped mortality as only part of the plant had burnt. *Eriophthalmus ericoides* was nearly eliminated from all burnt sites, with only two seedlings at a site in the Victoria West region, one seedling in the Hanover region, and a partially burnt individual in the Middelburg region together with a single *Ruschia intricata* plant (Table S.3). *Plinthus karooicus* and *Eriophthalmus spinescens* were

eliminated by fire and not found in any burnt areas. The nine remaining non-sprouter species occurred in very low numbers, except for *Melolobium candicans* at one site. Six occurred only in the Middelburg region. Fifteen new growth response classifications were made for previously unclassified species. Seven species were reclassified for responding differently from the classifications provided by du Toit et al. (2015). *Salsola calluna*, *Rosenia humilis*, *Trichodiadema pomeridianum*, *Amphiglossa tricephala* and *Helichrysum dregeanum* were classified as non-sprouters because they were never found in burnt plots. du Toit et al. (2016) classified these species as resprouters because resprouting individuals that had been found at their site. It appears, therefore, that species such as these may generally be killed by fire, and functionally are

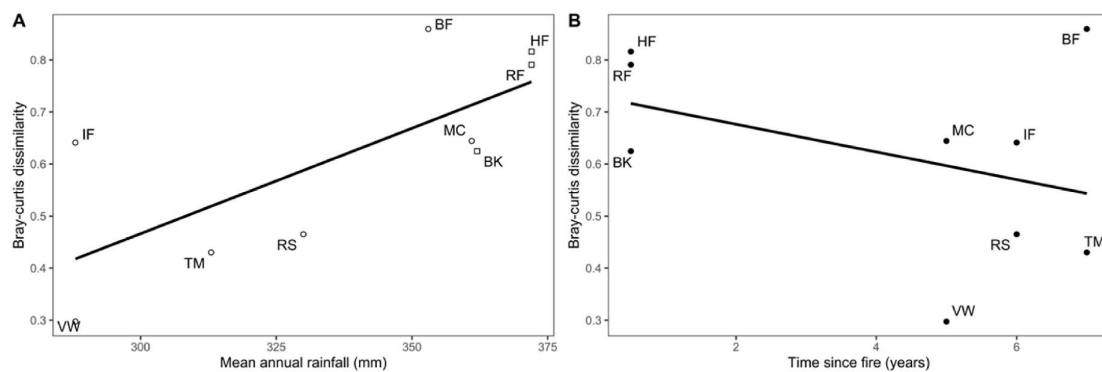


Fig. 3. Linear regression of Bray-Curtis dissimilarity indices against A) mean annual rainfall (mm) and B) Time since fire (years) for all fire sites. In A) Recently burnt sites are represented by open squares circles (<1 year since burn) and sites burnt a number of years previously are represented by open circles (>5 years). Each point represents a paired plot.

Table 2

Mean ($\pm$ SE) shrub canopy cover (cm^2), density (plants/m^2) and height (cm) for karroid dwarf shrubs in burnt and unburnt areas (* indicates $P < 0.05$, ** indicates $P < 0.001$ for paired t -test comparison between burnt and unburnt plots).

Site	Shrub canopy cover (cm^2)		Shrub density (plants/m^2)		Shrub height (cm)	
	Burnt	Unburnt	Burnt	Unburnt	Burnt	Unburnt
Victoria west commonage	2618 $\pm$ 518.2	2692.2 $\pm$ 645.1	1.8 $\pm$ 0.26	1.9 $\pm$ 0.32	21.5 $\pm$ 1.58	22.5 $\pm$ 1.93
Inverness	2356 $\pm$ 470.5	3417 $\pm$ 242.1 *	1.5 $\pm$ 0.12	1.8 $\pm$ 0.22	23.1 $\pm$ 0.83	22.1 $\pm$ 1.56
The Mills	2402 $\pm$ 436.2	2013 $\pm$ 292.3	1.9 $\pm$ 0.19	2.0 $\pm$ 0.24	18.9 $\pm$ 0.71	19.4 $\pm$ 1.71
Richmond siding	2590 $\pm$ 370.3	3226 $\pm$ 596.5	1.8 $\pm$ 0.3	1.9 $\pm$ 0.31	22.7 $\pm$ 1.44	24.2 $\pm$ 1.13
Brienne	2913 $\pm$ 1196.4	2502 $\pm$ 410.2	1.3 $\pm$ 0.25	1.6 $\pm$ 0.53	21.5 $\pm$ 1.34	15.2 $\pm$ 4.75
Middelburg commonage	2571 $\pm$ 807.2	3095 $\pm$ 609	2.2 $\pm$ 0.26	2.5 $\pm$ 0.36	23.6 $\pm$ 2.29	23.9 $\pm$ 2.28
Boesmanskop	6561.5 $\pm$ 1295.19	2824.39 $\pm$ 690.6	3.4 $\pm$ 0.69	1.87 $\pm$ 0.2 *	19.7 $\pm$ 2.44	31.14 $\pm$ 3
Helpmekaar	1557.4 $\pm$ 378.93	4779.17 $\pm$ 669.3 **	1.5 $\pm$ 0.08	1.28 $\pm$ 0.3	24.9 $\pm$ 0.63	18.94 $\pm$ 4.5
Redlands	3151.2 $\pm$ 776.04	3052.06 $\pm$ 345.6	2.1 $\pm$ 0.23	2.48 $\pm$ 0.4	21.6 $\pm$ 1.79	26.92 $\pm$ 3.5

therefore fire-intolerant, even though mortality may not be 100%. *Jamesbrittenia pinnatifida*, whose response was previously unknown, was classified as a resprouter.

Burning tended to affect the proportional cover of other functional types. Palatable leaf succulent shrubs >30 cm, found in unburnt areas, were not present in burnt areas (Table 3). Cover of unpalatable dwarf shrubs >30 cm and of palatable dwarf shrubs <30 cm was higher on burnt than on unburnt areas ($t = -1.9584$, $df = 24$, $P = 0.0619$; $t = -1.7811$, $df = 119$, $P = 0.0774$, respectively), indicating that these functional types may recover well following fire.

Despite no overall effect of burning on the proportional cover of palatable dwarf shrubs >30 cm, the proportional cover of sprouter species within this functional type was higher, and that of non-sprouter species lower, on burnt areas (Table 3). The proportional cover of sprouting shrubs was not different between burnt and unburnt plots. Proportional cover of non-sprouting, palatable dwarf shrubs <30 cm was lower on burnt than unburnt areas (Table 3).

The proportional cover of non-sprouting species was significantly lower than cover of sprouting species in both burnt and unburnt plots across all nine sites (Table 4). The proportional cover of non-sprouting shrubs (dwarf and regular) was significantly lower in burnt compared to unburnt plots ($t = 2.1314$, $df = 15$, $P = 0.0345$) but the proportional cover of sprouting shrubs (dwarf and regular) did not differ between burnt and unburnt plots ($t = 2.145$, $df = 14$, $P = 0.909$, Table 4).

4. Discussion

4.1. Community transformation

The effect of fire on vegetation has been extensively studied for some vegetation types (He et al., 2019), which can differ considerably in their

response to fire, and time taken to return to their pre-fire composition. In the Nama-Karoo, disturbances such as heavy grazing and drought usually take several years to induce significant changes in vegetation composition of perennial dwarf shrubs. Recovery (return to pre-disturbance composition) is very gradual owing to slow rates of recruitment as germination opportunities afforded by adequate rainfall are rare especially when in the presence of grazing (Milton, 1994). By contrast, fire causes a profound, sudden change in the composition of the shrub composition, with many species being instantly extirpated. The true history of fire on the Nama-Karoo plains is unknown, though evidence suggests that they were not subject to regular burning. This study revealed that fire has long-lasting effects in Nama-Karoo vegetation; burnt Nama-Karoo vegetation tended towards its pre-burnt state, but after nearly a decade was still more than 60% dissimilar to unburnt vegetation.

Life history strategy was pivotal in determining the nature and extent of impact by fire on karoo shrublands. This study confirmed preliminary findings that some Karoo shrub species are non-sprouters that are temporarily eliminated by fire, whereas most Karoo shrub species are sprouters whose adults are not killed by fire (du Toit et al., 2015a; 2015b). Non-sprouter species contributed on average 22% of the shrub cover of the unburnt communities that included dominant or abundant species such as *Eriocephalus ericoides*, *Eriocephalus spinescens* and *Ruschia intricata*. All were locally eliminated by fire. Abundance of fire-intolerant non-sprouter species is therefore an important determinant of the degree of community change resulting from a single fire. A negligible abundance of non-sprouter species on burnt sites up to eight years following fire suggests that these species possess a poor ability to recolonise. Indeed, these species would become locally extirpated if they failed to re-establish at all, resulting in a shrub community composed exclusively of sprouters. Such extirpations of several, often dominant

Table 3

The average relative cover of sprouter and non-sprouter species in each functional type as a proportion ($\pm$ SE) of total cover (cm^2/m^2) in burnt and unburnt plots, and associated paired *t*-test statistics.

Functional Type		Burnt	Unburnt	t	df	P
palatable dwarf shrub <30 cm	Sprouter	0.35 $\pm$ 0.059	0.25 $\pm$ 0.043	1.9454	127	0.0539
	Non-Sprouter	0.02 $\pm$ 0.009	0.07 $\pm$ 0.016	-2.6945	127	0.0080
palatable dwarf shrub >30 cm	Sprouter	0.29 $\pm$ 0.116	0.01 $\pm$ 0.007	2.3943	47	0.0207
	Non-Sprouter	0.13 $\pm$ 0.090	0.52 $\pm$ 0.162	-2.3955	47	0.0206
palatable leaf succulent shrub >30 cm	Sprouter		0.01 $\pm$ 0.013			
	Non-Sprouter		0.30 $\pm$ 0.100			
unpalatable dwarf shrub <30 cm	Sprouter	0.25 $\pm$ 0.060	0.20 $\pm$ 0.043	0.62763	63	0.5325
	Non-Sprouter	0.07 $\pm$ 0.068	0.09 $\pm$ 0.026	-0.3144	63	0.7543
unpalatable dwarf shrub >30 cm	Sprouter	0.27 $\pm$ 0.080	0.36 $\pm$ 0.086	-0.7256	24	0.4751
	Non-Sprouter		0.02 $\pm$ 0.021			
unpalatable parasitic dwarf shrub	Sprouter	0.28 $\pm$ 0.277	0.85 $\pm$ 0.699			
	Non-Sprouter					
unpalatable shrub	Sprouter	0.36 $\pm$ 0.104	0.21 $\pm$ 0.089	0.8360	12	0.4195
	Non-Sprouter					

Table 4

Mean ($\pm$ SE) proportional cover (cm^2/m^2) of non-sprouter and resprouter species (of dwarf and regular shrubs) in plots at burnt and unburnt sites.

	Proportion of total shrub (dwarf and normal) cover (%)	
	Burnt sites	Unburnt sites
Non-sprouter	11.1 $\pm$ 3.82	22.8 $\pm$ 2.51
Resprouters	49.0 $\pm$ 4.61	52.3 $\pm$ 11.5
t-value	2.12	2.25
Df	15	11
P value	0.001	0.037

species are characteristic of fire-naïve ecosystems (Pausas and Parr, 2018). Whether temporary elimination of some dominant species might allow less competitive species to persist or even flourish during the period before non-sprouter species re-establish will only be revealed by ongoing surveillance. This study has further contributed to understanding of the impact of fire on Nama-Karoo vegetation through increasing the pool of species classified as sprouters or as non-sprouters (Table S.3). At least 14 sprouting species benefitted from burning (Table S.3). Success of some species appears to be because of an extensive root system covering a large local area aiding the formation of a dense stand. Examples include the shrubs *Lycium cinereum* and the unpalatable *Asparagus retrofractus* at The Mills farm, and the unpalatable *Stachys rugosa* at the Boesmanskop site. Species of small stature also benefitted from removal of large shrubs, examples of which were increases in *Limeum aethiopicum* and *Felicia muricata* in the western sites of Inverness farm and Victoria West Commonage.

4.2. Implications of structural change

Changes in vegetation structure may portend reorganisation of a plant community that could influence ecosystem functioning and land use. Although shrub height, density and canopy cover after a fire were not uniform across the nine sites, fire did not have a pronounced effect on these variables because the nature and extent of their change depended on rainfall regime, history of grazing prior to a fire, and post-fire grazing pressure (Table S.2). Fire is expected to indirectly affect demographic performance of surviving shrub populations through altering their size structure, because survival, rate of vegetative growth and reproductive output of individual plants are usually positively related to size (Silvertown and Charlesworth, 2009).

Gaps created following reductions in shrub density, cover and height by a fire may be colonised by short-lived species that may temporarily dominate the landscape. For example, the short-lived grass *Aristida congesta* increased at the first fire site studied in the Karoo (du Toit et al., 2015b). A high cover of ephemeral species in burnt sites was further evidence that short-lived species benefit from an altered shrub structure. Similar patterns are observed in areas where shrub cover is reduced by overgrazing (Heukes and Cowling, 1999).

Four “Karoo dwarf shrub” functional types characterise the Karoo. The proportional cover of sprouters increased whereas that of non-sprouters became negligible for these four functional types, indicating that sprouters are replacing non-sprouters. Changes in canopy cover of these four types provide an estimate of available phytomass which can be used, with knowledge of species present, to predict carrying capacity of Nama-Karoo rangelands (du Toit, 1995). The availability of palatable shrubs declined across all three regions following fire to an extent expected to have implications for fodder flow for livestock ranching. Karoo graziers therefore face a new challenge of accounting for fire-induced changes in forage availability and palatability, changes that may impact regional economies if large areas become burnt. Grass is valuable fodder for livestock farmers, but its greater biomass variability than shrubs in relation to rainfall variability compromises fodder flow to livestock, especially during dry periods when the nutritive value of grass is low. By contrast, a stable forage source offered by long-lived karoo shrubs throughout the year (du Toit et al., 2009) is jeopardised by reduction of shrub abundance following fire, especially during drought periods when grass biomass is also severely reduced (du Toit et al., 2018).

4.3. Alternate vegetation states and biome shifts

A shift in the boundary between grassland and shrubland biomes has occurred in many parts of the world (Mucina, 2019). Acocks (1953) proposed that the Karoo is a degraded grassland that had been transformed through overgrazing by sheep and goats, postulating that palatable perennial grasses had been replaced by drought-tolerant, unpalatable shrubs. Consequently, the boundary between the Nama-Karoo and Grassland Biomes had moved up to 100 km eastward. Acocks' (1953) thesis had not considered long-term climatic variability. By contrast, others have recognised that this biome boundary is dependent on rainfall, and have shown long-term oscillation over the past millennium, with grassland shifting westward during periods of high rainfall, and Nama-Karoo encroaching eastward during dry periods (Mucina et al., 2006). This biome boundary appears to be currently shifting westward. A 15% increase in summer rainfall over the eastern Nama-Karoo since the 1950s, together with significant reductions in grazing pressure, has resulted in a dramatic increase in grass cover over the last 60 years (Masubelele et al., 2014, 2015). This pattern of change is consistent with already recognised effects of rainfall and grazing on vegetation dynamics in the eastern Upper Karoo (du Toit et al., 2018; Masubelele et al., 2014; O'Connor and Roux, 1995). Given predicted shifts in vegetation, particularly biome shifts, we need to consider the direct effects of novel fires, rainfall and grazing, and their interactions.

Long-term implications of the vegetation changes resulting from fire described in this study depend on whether apparent directional changes in rainfall will persist, whether fire will become commonplace, and whether fire will return to an already burnt area before Karoo shrub populations have recovered. In short, might Nama-Karoo shrublands manifest as an alternate stable state of grassland on account of fire as is argued for tropical grasslands that could support forest (Bond, 2019). The fires reported in this study could have covered extensive areas had they not been extinguished. Grassiness has increased over a large area (Masubelele et al., 2015) in response to increasing summer rainfall (du Toit and O'Connor, 2014; Harmse et al., 2021), suggesting that fire may become more frequent and affect larger areas, even those that experience continuous heavy grazing (Table 1).

Predicted increases in annual rainfall over the eastern Karoo as a consequence of climate change (Engelbrecht et al., 2009) are consistent with observed change at one location (du Toit and O'Connor, 2014), a change that has favoured perennial grasses at the expense of dwarf shrubs, even in the absence of fire (du Toit et al., 2018). Increased amounts of grass fuel are the ostensible reason for the novel occurrence of fires on the plains of the Nama-Karoo since 2010 (du Toit et al., 2015a). This study has shown that dwarf shrub species decline conspicuously, dramatically so for non-sprouter species (Table 4), if subjected to an individual fire. Climate change predictions therefore suggest that suitable conditions will be created for an increased incidence of fire and for the reoccurrence of fire at locations previously burnt. Ignition should not prove to be a constraint because the eastern Karoo receives more lightning strikes per unit area than other area of the Nama-Karoo (Manry et al., 2013), as well as inevitable ignition by humans. In years of high grass biomass resulting from high rainfall, the chance of successful fire spread following ignition is increased (Engelbrecht et al., 2009; MacKellar et al., 2014).

The current constellation of factors has created the potential for a positive-feedback cycle to develop. Each fire could further reduce shrubs, thereby promoting grass, that would increase the likelihood of fire returning. Fire-return interval would be critical for long-term trend of vegetation change. Karoo shrubs are slow growing although the time taken for these species to reach maturity, produce seeds, and regenerate is unknown. A fire-return interval shorter than the maturation period of non-sprouting species would ensure their continued absence, as well as disrupting regeneration processes of sprouting species, thereby amplifying compositional and structural change. Direct effects on plants would be exacerbated by indirect effects on their environment and inimical to their performance - a decrease in canopy cover with each fire results in reduced infiltration and less soil moisture (Mills et al., 2009), and reduced availability of a suitable microclimate for shrub germination and establishment (Milton and Dean, 1995). This pattern of a positive feedback process may potentially lead to an alternate state of grassland in place of dwarf shrubland, that is, a shift to true grassland, which occurs to the north-east.

Successful land management in the eastern Karoo will depend on the ability of managers to recognise the significance of infrequent events such as fire (Wiegand et al., 1995). The loss of shrub diversity and changes in shrub community composition and structure will affect ecosystem functioning, especially the provision of a stable forage source for livestock and other herbivores. Changes in ecosystem functioning resulting from a change from a shrub- to a grass-dominated state require further investigation, and the spatial extent of this change has yet to be defined. If the boundary between the Grassland and Nama-Karoo Biomes moves westward, which may currently be the case, fire will be a major driver of the balance between soft-bodied grasses and woody plants. A shift from shrub-dominated to grass-dominated rangeland caused by fire could drive a shift in the biome boundary between the Grassland and Nama-Karoo Biomes. Fire should therefore be considered along with grazing and rainfall as an important driver of vegetation change in the Nama-Karoo.

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CRediT authorship contribution statement

L. Hebbelmann: designed the study, collected and analysed data, interpreted analyses and wrote the paper. **T.G. O'Connor:** contributed to the conception and design of the study, interpretation of the analyses of the paper and contributed to revision of the paper. **J.C.O. du Toit:** identified an opportunity for this study, took part in data collection, analysis, interpretation, and contributed to revision of the paper.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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The influence of grass competition and soil moisture on the growth and phenology of Karoo shrubs in the Eastern Upper Karoo

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Rainfall in the Nama-Karoo is sporadic and a plant's ability to access and utilise available soil moisture will determine its ability to persist in the system and to successfully recruit. When summer rainfall in the Eastern Karoo increases, grassiness increases at the expense of shrub canopy cover. This may drive a transition from shrubland toward grassland. The effect of grass–shrub competition on shrub growth and phenology in the Eastern Karoo is not adequately explained by the root–niche separation hypothesis or the succession hypothesis. In an experiment, we measured shrub growth and phenology in the absence (clipping treatment) and presence (control treatment) of grass over the 2017/2018 rainfall season. Grass clipping changed grass species composition over this period, but grass clipping did not benefit shrubs. We found no competitive effect of grasses on shrubs. However, shrub canopy cover showed a strong linear response to soil moisture, as did canopy cover to temperature. Similarly, soil moisture and temperature were important for stem growth and shrub phenology. Patterns of shrub growth and phenology in response to summer and winter rainfall provide important insight for land managers for optimising production while enabling phenological processes that allow recruitment to take place.

Keywords: competition, Karoo shrubs, phenology, soil moisture, state change

Introduction

Competition has emerged as a key paradigm for explaining the organisation of plant communities in semi-arid systems (Westoby 1980; Fowler 1986; Kunstler et al. 2016). The growth of plants in arid and semi-arid communities is at least partially controlled by interference from neighbours (Casper and Jackson 1997; Hamilton et al. 1999; Fowler 1986) and competition for soil moisture is widely recognised as an overriding determinant of plant community structure in arid and semi-arid regions, further modified by herbivory (Van Auken 2000). Water inputs to the soil in semi-arid and arid systems occur predominantly as small infrequent events, providing a pulse of water availability to a plant community. Wet soil dries quickly through evapotranspiration and plants compete for water with each other, thus the response time of shrubs to water input may be an important functional attribute (Midgley and Heyden 1999). The pulse–reserve conceptual model describes a simple relationship between rainfall, shrub growth and persistence. Rainfall triggers pulses of plant growth, reproduction or energy storage in roots (Reynolds et al. 2004). Growth response and resource-use efficiency varies amongst plant functional types (Kunstler et al. 2016), and influences competition in a community. Competition for resources during pulse events has consequences for an individual's ability to persist, grow and reproduce. Above-ground competition for light is also important in semi-arid shrub–grass communities (Krueger-Mangold

et al. 2004). Small stature and slow-growing individuals experience higher levels of competition for light in grass–shrub communities (Krueger-Mangold et al. 2004).

Most explanations for the coexistence of shrubs and grasses in arid areas have focused on available water (Walter and Mueller-Dombois 1971; Westoby 1980; Roux and Vorster 1983). Despite such a focus, there is no general consensus of the mechanisms for promoting the coexistence of these growth forms. Hypotheses range from reducing (maybe avoiding) competition for resources through root–niche separation, to variations in grass–shrub ratios with rainfall seasonality (Walker and Noy-Meir 1982). The root–niche separation model suggests that competition for resources is prevented because shrubs are deep rooted while grasses root more shallowly (Walter and Mueller-Dombois 1971; Walker and Noy-Meir 1982). Shrubs generally have deeper roots than grasses and it is widely accepted that shrubs can access water deeper in the soil profile (Reisman-Berman 2007; Walker et al. 1981). However, when moisture in deep soil layers is regularly depleted, some woody plants spread their roots laterally and occupy the upper soil layers in a similar rooting fashion as grasses (Hipondoka et al. 2003). This response highlights the importance of the availability of water to each group of plants spatially and temporally. Water availability is expected to be important in determining whether grasses can competitively exclude shrubs in the Nama-Karoo,

resulting in a shift from shrubland to grassland. If niche partitioning is absent, then it is expected that shrubs and grasses are equally able to utilise water that enters the soil, then water loss or the amount of precipitation received in a rainfall event may be the most important factor in competition between grasses and shrubs (Golluscio et al. 1998).

Karoo shrubs have a generalised type of root system with extensive vertical and horizontal distribution in the soil profile but there are often large differences between shrub species and among individuals of the same species (Cowling and Roux 1987). Based on the excavation of one specimen of each growth form in an area, Midgley and Heyden (1999) concluded that while there are some grass roots deep down in the profile, the majority of both shrub and grass roots are in the surface layers of the soil. They concluded that shrubs and grasses are competing for resources in the same layers of the soil and concur with a number of studies which suggest that the competitive balance between the two growth forms is maintained by the dependence of grasses on summer rainfall and shrubs on autumn/winter rainfall (Roux and Vorster 1983; Midgley and Heyden 1999).

In the Nama Karoo, rainfall and soil moisture are widely accepted as the factor which determines competitive interactions between shrubs and grasses (Milton 1992; Carrick 2003). When summer rainfall is higher than the long-term mean in the Nama-Karoo, grass cover increases at the expense of shrub basal cover (Hoffman and Cowling 1990; du Toit et al. 2018). If grassiness continues to increase in the Eastern Nama-Karoo and grasses are able to outcompete shrubs, then the result will be a transition from mixed grass-shrub vegetation to grass-dominated vegetation (Milton and Hoffman 1994). Two hypotheses have been presented to explain competition between grass and dwarf shrubs in the Eastern Karoo. Hoffman and Cowling (1990) and Milton and Hoffman (1994) proposed a cyclical model of succession in the eastern Karoo in which the rapid response of grasses to high summer (or annual) rainfall results in a corresponding decline in dwarf shrubs. They suggest that morphological traits of grasses, taller growth and generally shallower, more extensive root systems, enable grasses to out-compete the dwarf shrubs for both light and moisture. Where the grass stand is dominated by short grass species such as *Aristida congesta* or *Tragus* species, competition for light between shrubs and grasses will be low. In areas where tall, tufted grasses such as *Digitaria eriantha* or *Themeda triandra* dominate, many small-stature shrubs will experience high levels of shading, which may inhibit their photosynthetic ability and ultimately growth and reproductive abilities (Sardans et al. 2006; Kambatuku et al. 2011). Unfortunately, neither of these studies directly tested competition between shrubs and grasses and are based on detailed observations of communities. Their suggestions highlight the need to conduct field experiments to observe any competitive interactions between grasses and shrubs. Furthermore, the phenological responses of how individual shrub species respond to rainfall in the grassier eastern Karoo are unknown. In the eastern upper Karoo, grass abundance increases during periods of high rainfall and decreases during periods of low rainfall (Hoffman and Cowling 1990;

du Toit et al. 2018). It is therefore important to understand how shrubs might respond to either high or low grass abundance. The reduction or elimination of one growth form should lead to a response from the other.

In this study we assess shrub herbage growth and phenology in response to soil moisture and grass competition. Soil moisture provides a more accurate indication than precipitation of the moisture directly available to plants. This is important because volumetric soil moisture may not be proportional to rainfall owing to differences related to storm size in evaporation, overland flow and deep drainage (Edwardes 2018). We anticipate that, in the absence of grasses, shrubs will experience decreased levels of competition for soil moisture that should enable them to grow and reproduce at a rate higher than shrubs in the presence of competing grasses. The implications of this are far reaching in an area where livestock production depends on rangeland productivity. The removal of one functional type should benefit the other functional type if they interact competitively (Fowler 1986). The importance of the timing of rainfall can also be examined in such experiments, if a species can commence growth earlier in the season it may have an advantage over species that commence growth later, and therefore have less time to increase in size and reproduce. Regular monitoring further affords an opportunity to closely monitor plant phenology and growth over time, in order to better understand the response of plant groups to resource availability and niche partitioning among such groups of plants (Fowler 1986).

Methods and Materials

Study area

The experiment was conducted at the Grootfontein Agricultural Development Institute outside Middelburg (31°28'41.7" S, 25°01'12.0" E; 1264 m amsl) in the Eastern Cape, South Africa. The mean annual rainfall for Grootfontein over the past 20 years is 445 mm, ranging between 193 and 727 mm (du Toit 2010). Warm (summer) months and cold (winter) months were classified according to the average daily temperature. Months with an average daily temperature above 15 °C were classified as warm months (October to April), whereas months with an average daily temperature below 15 °C were classified as cold months (May to September).

Geology is of the Katberg Formation of the Tarkastad Subgroup, with level valley floors of quaternary alluvial deposits and hills predominantly of sandstone (Woodford and Chevallier 2002). Soil at the site is a slightly brackish (pH = 5.7) sandy clay loam (sand = 60%, clay = 29%, silt = 11%). Average soil depth in the vicinity of the experimental site was 50 ± 25.3 (SE) cm (Van Lingen M, Afrikaner-Hereford grazing trial, pers. comm., 2017).

The site was in the Eastern Upper Karoo (Mucina et al. 2006), a grassy shrubland dominated by Karoo dwarf shrubs, mainly *Erioccephalus ericoides*, *Erioccephalus spinescens* and *Ruschia intricata*, interspersed among perennial and annual grass species. The experiment was conducted in rangeland considered to be in excellent condition (du Toit 2002). Livestock were excluded from the

experimental site, but the absence of small herbivores such as hares, tortoises and steenbok (*Raphicerus campestris*) could not be guaranteed.

Data collection

The experiment was laid out as a single randomised block. Six 3 m × 3 m plots, each surrounded by a 1.5 m wide buffer, were marked out in an area with approximately uniform species composition determined by preliminary sampling. This experiment was initiated on the 15 October 2017 and terminated on the 30 November 2018. Three plots were subjected to complete grass defoliation by clipping, maintained throughout the experimental period. Weekly clipping severely stunted grass growth and little clipping was needed from the eighth week onwards, even during periods of high rainfall. The remaining three plots were control plots. Each month, all shrubs within the plots were measured for height, canopy longest diameter (r), the corresponding perpendicular diameter (q), and the proportion of the canopy bearing leaves. Reproductive state (flowering, seeding, non-reproductive) was recorded for each individual measured.

Grass and herbaceous species were sampled at the start (October 2017) and at the end of the experimental period (November 2018). Three 1 m × 1 m quadrats were sampled in each plot. Percentage cover of each grass and herb species in each quadrat was estimated visually. Plant nomenclature follows Klopfer and Winter (2019). The leaved canopy cover of each shrub, hereafter referred to as canopy cover, was calculated using the formula:

$$A = \left[\pi \left(\frac{r}{2} \right) \left(\frac{q}{2} \right) \right] L$$

where r and q are perpendicular canopy dimensions and L is the proportion of the canopy bearing live leaves. Three plants each of *E. ericoides*, *E. spinescens* and *R. intricata* within each plot were marked (although only two rather than three plants of one species were present). Three stems were marked on each plant using colour-coded plastic cable-ties. The length of each stem was measured monthly over the experimental period. Average growth for each species in each plot was used to describe stem growth over time.

Soil moisture, measured using an UMS Theta Probe ML3, was obtained from eddy covariance flux towers at two sites (run by the ARS AfricaE and EMSAfrica projects), approximately 200 m and 700 m away from the experimental site

An average of soil moisture values measured at 10 cm and 20 cm was used in the analysis. Data from the closer site was used, but when data were missing, due to technical error, data from the further site (Tower two) was used. Data from the two sites were highly correlated ($F_{(1,609)} = 4763$, $p < 0.0001$, $R^2 = 88.7\%$) and a patched datum was calculated using the following formula before being substituted into the dataset:

$$x = 0.02293788 + (1.07473 \times \text{Karoo2})$$

where x is the adjusted value for each missing data point and Karoo2 is the corresponding value from Tower two.

Data were separated according to season based on rainfall and temperature. January, February, March, April, October, November and December were classified as summer months. The average daily temperature and average monthly rainfall in these months is significantly higher than those of the dry, cold winter months of May, June, July, August and September.

Statistical analysis

All analyses were carried out using the R base package in Rstudio (RStudio Team 2016) and ggplot2 was used to create figures (Wickham 2016). A Student t -test was used to test for overall change in grass and shrub canopy cover, and the cover of individual grass and shrub species between the beginning (October 2017) and the end of the experiment (November 2018).

Analysis of variance was used to compare the change in live canopy cover of grass, shrubs and grass functional types in clipped and control treatments over the fourteen-month experimental period. Functional types were determined based on palatability and life strategy. Productive more palatable species of grass were classified as palatable perennial, less productive less palatable grass species were classified as unpalatable perennial and annual or otherwise short-lived grasses were classified as short-lived grasses. A general linear model was used to analyse how the removal of grass biomass (clipping), average daily soil moisture, and average daily temperature affected canopy cover of karoo shrubs.

To determine how average soil moisture affected shrub canopy cover, we calculated the month-on-month change, referred to as monthly change, in shrub canopy cover of all shrubs in the experimental area between each sample date over the experimental period and examined this change in relation to soil moisture using a linear regression. Thereafter, the average monthly change in shrub canopy cover relative to average daily soil moisture was then analysed separately for summer and winter using a linear regression. Sample size allowed for the examination of how canopy cover of the five most abundant shrub species in the experiment changed month on month in relation to average daily soil moisture and average daily temperature for each month using a linear regression.

The average stem length of marked *E. ericoides*, *E. spinescens* and *R. intricata* stems over the experimental period was separately compared between control and clipped treatments using t -tests. We calculated the monthly change in stem length, and a linear regression was used to examine the relationships between average stem length change, average daily soil moisture and average daily temperature.

An analysis of variance was used to compare the average monthly proportion of plants flowering, seeding and budding in the control and clipped treatments separately for *E. ericoides*, *E. spinescens* and *R. intricata*. A general linear model was used to test for the effect of treatment and rainfall on the proportion of shrubs of each species that were flowering and seeding each month. Thereafter linear regressions were used to explore how the change in the proportion of plants flowering and seeding each month related to average daily soil moisture.

Results

Soil moisture and shrub growth

Rainfall received over the period of the experiment (Figure 1) measured 590 mm away from the experimental site, resembled an average pattern of rainfall for the area with most rain falling during the second half of the summer into early winter. Rainfall at the study site was received during late summer and early winter with 50% of the total rainfall received in January and February 2018. Soil moisture fluctuated over the experimental period and was closely associated with rainfall (Figures 1 and 2). Soil moisture was measured at $0.081 \text{ cm}^3 \text{ cm}^{-3}$ at its lowest and at $0.407 \text{ cm}^3 \text{ cm}^{-3}$ at its highest. Average daily soil moisture in winter ($0.144 \text{ cm}^3 \text{ cm}^{-3}$) was only 1% higher than the average daily soil moisture in summer ($0.143 \text{ cm}^3 \text{ cm}^{-3}$), owing to a dry start (October to December) to summer rains, good rains in late summer–early winter, as well as additional rain during late winter. Isolated rainfall events below 3 mm did not result in a change in soil moisture but multiple small rainfall events of between 3 mm and 4 mm resulted in a measurable and accumulative increases in soil moisture. During winter months soil moisture remained higher for several days longer than after the same amount of rain during the summer months. For example, soil moisture took 32 days to return to its pre-rain level after 23.8 mm of rain fell during winter; whereas, in summer, soil moisture returned to pre-rain levels 12 days after 16.5 mm of rain. The recharge in soil moisture is not proportional to the volume of follow up rainfall events. The total rainfall during the height of winter from May to September was only 4 mm.

The average monthly change in shrub canopy cover was influenced by soil moisture and not by average daily temperature (Table 1; Figures 3 and 4). Despite an insignificant linear relationship between monthly change in canopy cover and average daily temperature, there appeared to be a seasonal influence of temperature on shrub cover change (Figure 4). The effect of treatment, and its interaction with average daily soil moisture and with average daily temperature, on shrub canopy were not significant and were therefore excluded from the model. Over the entire experimental period, only soil moisture had an effect, but the model accounted for only 9% of the variance. In the model for summer only soil moisture positively influenced growth, with the model accounting for 13% of the variance. During winter, temperature did not have a positive influence on shrub canopy cover and despite conspicuous variation in soil moisture during the winter months, soil moisture did not influence changes in shrub canopy cover.

The most common species in the experiment did not show a uniform response in the way their canopy cover changed over time in response to soil moisture and temperature. The monthly changes in the average canopy cover of *Pentzia globosa* and *R. intricata* was positively affected by soil moisture ($F_{(1,37)} = 5.143$, $p = 0.027$ and $F_{(1,76)} = 9.568$, $p = 0.003$, respectively), but unaffected by daily temperature ($F_{(1,37)} = 2.523$, $p = 0.116$ and $F_{(1,76)} = 0.108$, $p = 0.743$, respectively). The monthly change in the average canopy cover of *E. ericoides*, *Phymaspermum parviflorum* and *E. spinescens* were unaffected by neither average daily soil

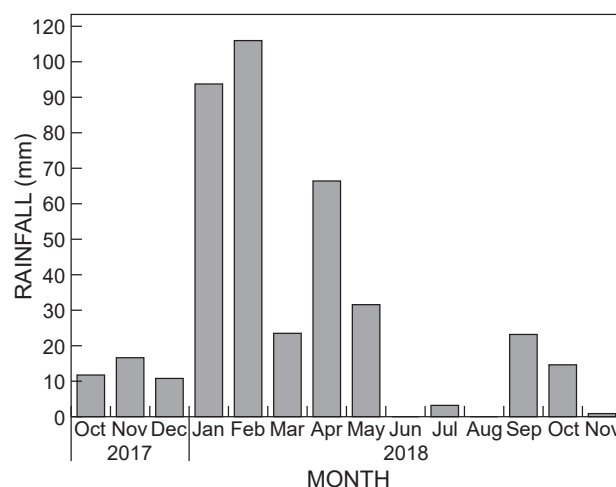


Figure 1: Total monthly rainfall at the experimental site for the period of the experiment

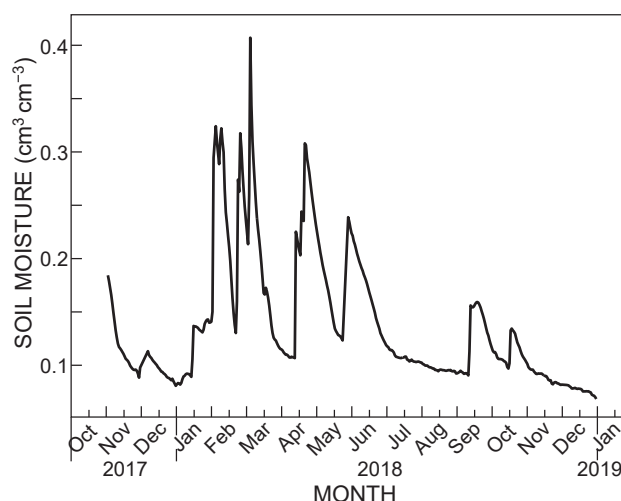


Figure 2: Average daily soil moisture ($\text{cm}^3 \text{ cm}^{-3}$) at the experiment site for the period of the experiment

Table 1: Linear regression coefficients with SE in parentheses, for variables predicting monthly change in average shrub canopy cover (cm^2) per plot over the entire experimental period, summer months and winter months

	All months	Summer	Winter
No. observations	76	45	27
Soil moisture ($\text{cm}^3 \text{ cm}^{-3}$)	930.6* (367.74)	1009.1* (475.09)	449.6 (651.32)
Temperature ($^{\circ}\text{C}$)	3.7 (4.03)	10.5 (13.39)	30.3 (21.53)
Intercept	-203.2* (-8.28)	-342.4 (231.24)	-387.2 (215.98)
R^2	0.0935	0.1325	0.0995
Adjusted R^2	0.0693	0.0939	0.0328

* $p < 0.05$

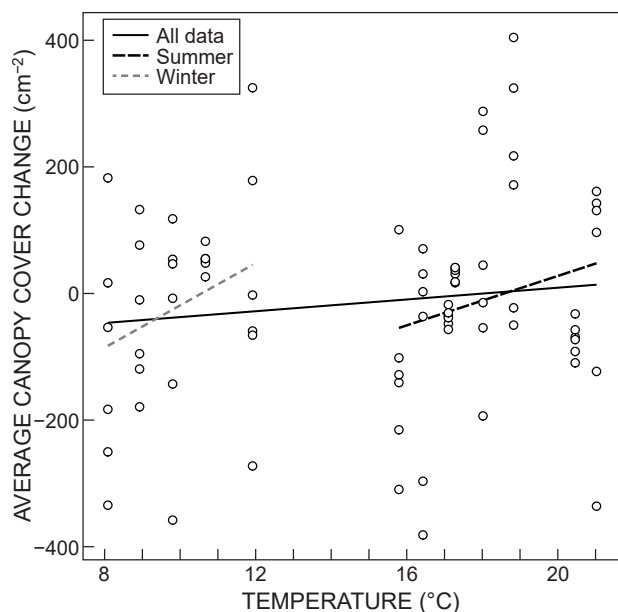


Figure 3: Average monthly change in average canopy cover (cm^2) per plot according to average daily temperature ($^{\circ}\text{C}$). Lines show the linear relationship between cover and temperature during winter, summer and for the full experimental period

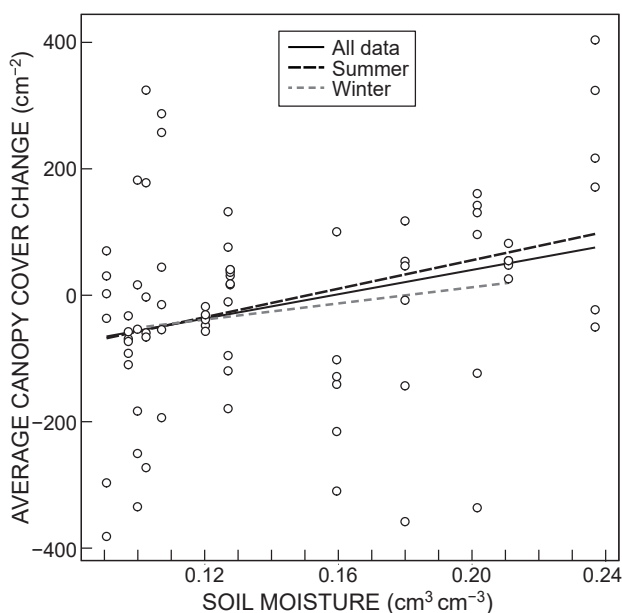


Figure 4: Average monthly change in average canopy cover (cm^2) per plot according to average soil moisture ($\text{cm}^3 \text{cm}^{-3}$). Lines show the linear relationship between soil moisture during winter, summer and for the full experimental period

moisture ($F_{(1,76)} = 0.001$, $p = 0.973$, $F_{(1,50)} = -0.127$, $p = 0.723$ and $F_{(1,76)} = 0.877$, $p = 0.352$, respectively) nor by average daily temperature ($F_{(1,76)} = 0.558$, $p = 0.457$; $F_{(1,50)} = 1.456$, $p = 0.232$ and $F_{(1,76)} = 0.041$, $p = 0.840$, respectively).

Grass and shrub cover

Continued removal of above-ground grass biomass changed grass species composition. Cover of the short-lived species *Tragus racemosus* increased by 63%, causing a significant increase in the cover of short-lived grasses in clipped plots (Table 2). Regular clipping resulted in the death of *T. triandra*, *D. eriantha*, *Eragrostis obtusa* and *Eragrostis curvula*, while the cover of *Aristida diffusa* and *Tragus koelerioides* increased in clipped plots (Table 2). Despite increases in cover of some of the unpalatable grass species there was no overall effect of clipping on unpalatable perennial grasses (Table 2; Figure 5). Although shrub canopy cover fluctuated over the duration of the experiment (Figure 6), grass removal by regular clipping had no effect on overall shrub canopy cover or on the cover of any individual shrub species (Table 2).

Stem growth

The average stem length across the three most abundant shrub species, *E. ericoides*, *E. spinescens* and *R. intricata*, did not change over the experimental period and there were no significant differences in average stem length between clipped and control treatments ($t = 1.154$, $F = 5$, $p = 0.343$). When examined separately, the removal of grass by clipping did not affect the average stem length of *E. ericoides* ($t = 1.717$, $F = 5$, $p = 0.26$), *E. spinescens* ($t = 1.717$, $F = 5$, $p = 0.0758$) or *R. intricata* ($t = 0.079$, $F = 5$, $p = 0.792$). Despite seasonal fluctuation in length caused by the loss of apical leaves in some individuals during the cold winter months (Figure 7), there was no significant influence of soil moisture on stem length across the three species over the entire experimental period (Table 3). When stem length is pooled for the three species there was, however, a significant effect of the interaction between soil moisture and temperature on stem growth over the experimental period ($p < 0.05$). During summer months there was a significant linear relationship between soil moisture and growth while temperature had no significant influence (Table 3). During winter months temperature and the interaction between soil moisture and temperature had a significant linear relationship with stem growth (Table 3).

When assessed separately, the effect of soil moisture, temperature and the interaction between soil moisture and temperature was not consistent across the three species. *Erioccephalus ericoides*, *R. intricata* and *E. spinescens* showed conspicuously individualistic responses to variation in soil moisture and temperature. Soil moisture and the interaction between soil moisture and temperature had a significant effect on stem growth of *E. ericoides* individuals during winter, and over the entire experimental period (Table 4) but there was no effect of soil moisture or temperature on stem growth of *E. ericoides* during summer (Table 4).

Temperature had no significant effect on stem growth of *E. spinescens*, but soil moisture had a significant effect during summer and over the entire experimental period. Soil moisture did not affect stem growth of *E. spinescens* in winter (Table 4).

Soil moisture interacted with temperature to significantly affect *R. intricata* stem growth over the experimental period (Table 4). During summer, stem growth and soil moisture resulted in a significant increase in stem growth.

Table 2: Change in percentage canopy cover of grass, shrub and herbaceous species over the duration of the clipping trial. * indicates a significant t-test result ($p < 0.05$) for the change in canopy cover between the start and end of the experiment

	Percent cover in clipped plots			Percent cover in control plots	
Growth form/species	Start	End		Start	End
Short-lived grasses	4.9	4.5		5.4	2.2
<i>Tragus racemosus</i>	4.1	6.7	*	1.8	1.4
<i>Aristida congesta</i>	5.7	2.3		9.0	3.0
Palatable perennial grasses	6.7	1.8	*	6.8	7.5
<i>Digitaria eriantha</i>	8.3	0.0	*	3.1	4.4
<i>Eragrostis curvula</i>	7.0	0.0	*	10.0	7.6
<i>Themeda triandra</i>	4.5	0.0	*	9.6	12.0
<i>Eragrostis lehmanniana</i>	7.0	7.1		4.3	6.1
Unpalatable perennial grasses	3.4	4.0		4.9	5.9
<i>Aristida diffusa</i>	3.7	8.3	*	6.4	8.1
<i>Eragrostis obtusa</i>	3.7	0.0	*	6.4	9.0
<i>Oropetium capense</i>	3.0	2.3		3.2	3.0
<i>Tragus koelerioides</i>	3.0	5.3	*	3.4	3.6
Herbaceous and geophyte species	1.7	2.4		2.6	2.2
Geophyte species	0.0	3.8		1.5	0.9
<i>Cyperus</i> spp.	2.0	1.8		1.9	0.6
<i>Oxalis</i> spp.	1.5	2.3	*	4.1	5.0
<i>Indigofera alternans</i>	3.4	1.5		2.8	2.3
Perennial dwarf shrubs	11.1	11.1		11.1	11.1
<i>Eriocephalus ericoides</i>	10.4	10.4		14.9	17.3
<i>Eriocephalus spinescens</i>	38.0	35.0		24.7	20.7
<i>Felicia muricata</i>	0.0	1.8		1.6	3.2
<i>Pentzia globosa</i>	19.3	18.2		18.5	19.2
<i>Phymaspermum parviflorum</i>	5.8	0.0		1.9	0.0
<i>Ruschia intricata</i>	25.2	29.0		28.6	25.1
<i>Selago geniculata</i>	1.3	5.8		0.0	4.8
<i>Thesium hirtum</i>	0.0	0.0		1.4	1.1
<i>Lycium cinerarium</i>	0.0	0.0		8.3	8.6

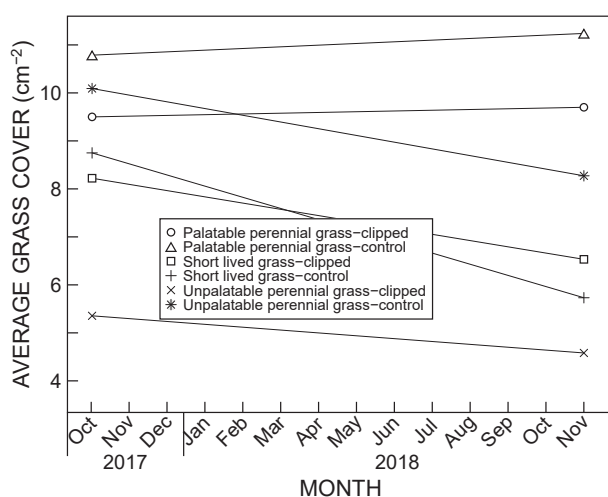


Figure 5: Average cover of grass in clipped and control treatments over time. Clipping was not necessary from December 2018

During winter the interaction between soil moisture and temperature on stem growth was significant (Table 4). During the winter months several *R. intricata* individuals lost

their leaves, but these regrew when temperatures and soil moisture increased (Table 4).

Stem length changes were affected mainly by the presence or absence of apical leaves. All three species showed signs of seasonal deciduousness clearly demonstrated by seasonal changes in average canopy cover (Figure 7). Variation was greatest in *E. ericoides* and *R. intricata*, 13.8% of individuals of these species were deciduous, whereas only 2.7% of *E. spinescens* were deciduous.

Shrub phenology

The monthly average proportion of shrubs in flower, seed and bud was not affected by the removal of above-ground grass biomass. The proportion of *E. ericoides*, *E. spinescens* and *R. intricata* individuals flowering, seeding and in bud was also unaffected by the removal of above-ground grass biomass (Table 5).

Flowering and seeding activity were significantly influenced by average daily soil moisture. The proportion of plants flowering ($F_{(1,74)} = 6.971$, $p = 0.01$) and seeding ($F_{(1,74)} = 12.925$, $p > 0.001$) were higher in months with higher average daily soil moisture. The proportion of plants flowering was positively related to the interaction between temperature and soil moisture while seeding was unaffected. Budding was unaffected by soil moisture and peaked during October and November 2017.

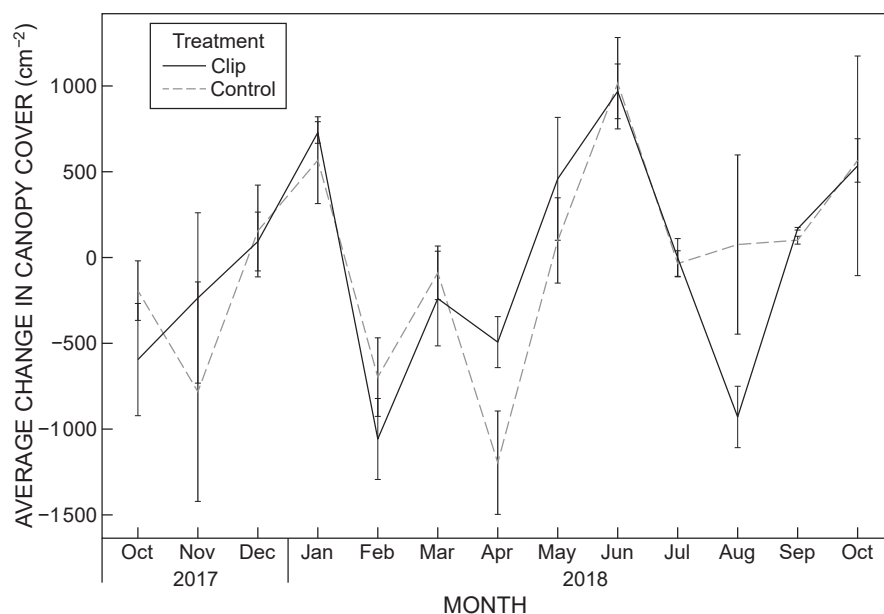


Figure 6: Change in average canopy cover (cm²) ± SD of shrubs in clipped (dashed) and control (solid line) treatments over the duration of the experiment

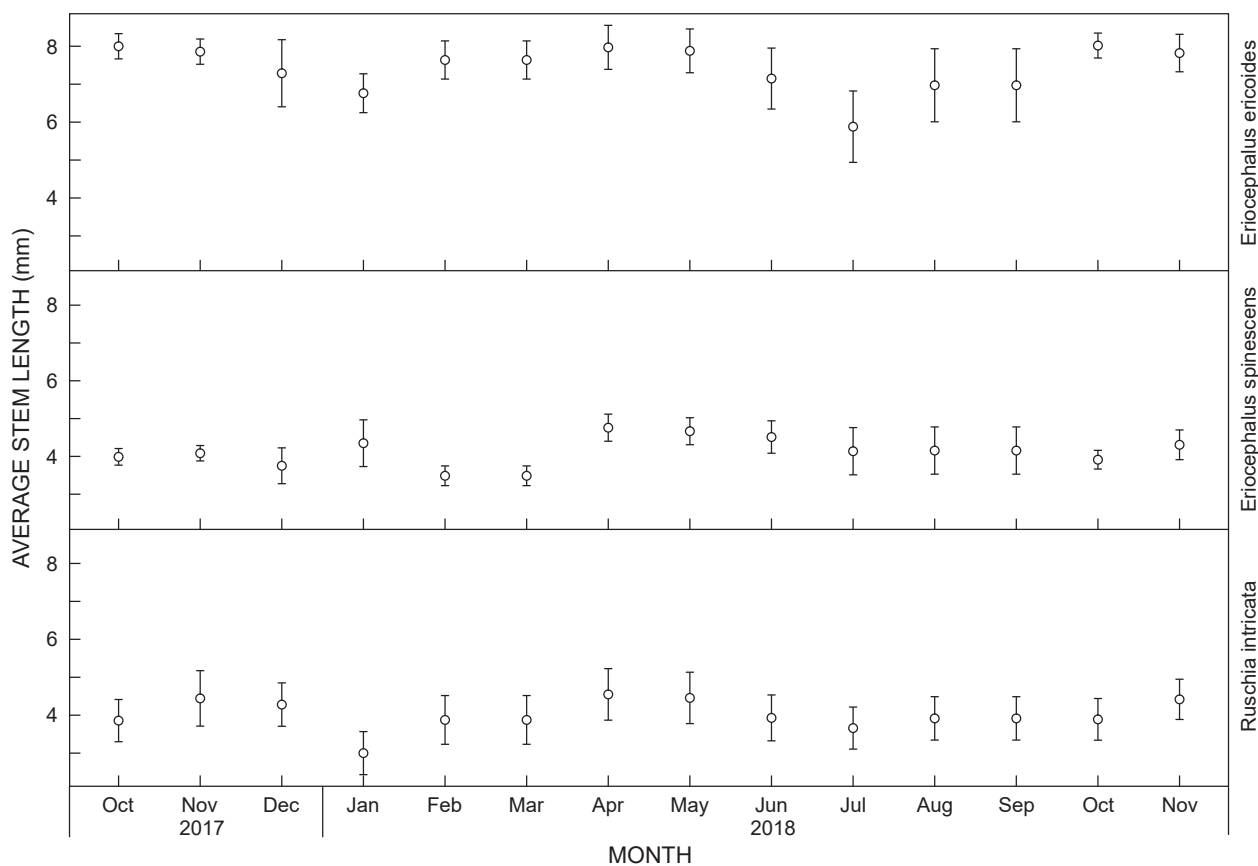


Figure 7: Average stem length (cm ± SD, n = 27) for the three most abundant species over the experimental period

The phenology of the three most abundant species differed over the experimental period (Figure 8). *Eriocephalus ericoides* individuals flowered in 13 months out of the 14-month observation period with a peak in the proportion of individuals flowering during the winter months, with 80% of individuals flowering during June 2018 (Figure 8). *Eriocephalus ericoides* individuals bore seed throughout the entire experimental period peaking during the winter months (Figure 8) and budding occurred during the summer months.

The proportion of *E. spinescens* flowering and seeding was high from December 2017 to May 2018, a pattern that was closely associated with soil moisture and coincided with the rainy season, with a sudden increase in September 2018 after rain. When average daily soil moisture was high the proportion of *E. spinescens* plants flowering and seeding was high ($F_{(1,22)} = 4.241$, $p = 0.051$; $F_{(1,22)} = 4.497$, $p = 0.045$; Figure 6). Budding was not affected by soil moisture but instead peaked at the beginning of summer. Average daily temperature had no effect on the proportion of *E. spinescens* individuals flowering, seeding or budding.

The proportion of *R. intricata* plants flowering was highest during summer but was not significantly affected by average

daily soil moisture ($F_{(1,24)} = 0.004$, $p = 0.947$). Seeding however, was influenced by soil moisture and was highest when average daily soil moisture was high ($F_{(1,24)} = 9.662$, $p = 0.0048$). Budding was unaffected by soil moisture or average daily temperature and was highest at the beginning of summer (Figure 8).

Discussion

Grass–shrub competition

We found no evidence showing competition between shrubs and grasses in our experiment. Furthermore, we found no support for either of the two hypotheses explaining shrub–grass competition in the Nama-Karoo. Hoffman and Cowling (1990) and Milton and Hoffman (1994) proposed a cyclical model of succession in the eastern Karoo in which the rapid response of grasses to high summer (or annual) rainfall results in a corresponding decline in dwarf shrubs. They suggest that morphological traits of grasses,

Table 5: Analysis of variance results for the influence of grass removal versus control on the average monthly proportion of Karoo shrubs, and three Karoo shrub species *Eriocephalus ericoides*, *Eriocephalus spinescens* or *Ruschia intricata* flowering, seeding and budding each month over 14 months, $df = 1,4$ for all F -values

Species/Functional type and residuals	Sum Sq	Mean Sq	F-value	Pr(>F)
All shrubs				
Flowering	225.3	225.3	2.709	0.174
Seeding	282.6	282.6	2.246	0.208
Budding	70.6	70.7	0.800	0.422
<i>Eriocephalus ericoides</i>				
Flowering	276.6	276.6	2.086	0.222
Seeding	185.2	185.2	0.730	0.440
Budding	36.6	36.58	0.372	0.575
<i>Eriocephalus spinescens</i>				
Flowering	132.1	132.1	5.594	0.099
Seeding	77.3	77.3	1.844	0.268
Budding	4.1	4.1	0.870	0.789
<i>Ruschia intricata</i>				
Flowering	0	0	0	1.000
Seeding	112.0	112.0	1.225	0.330
Budding	9.1	9.1	0.250	0.643

Table 3: Linear regression results, with SE in parentheses, for variables predicting monthly change in average stem length (cm) per plot, combined for *Eriocephalus ericoides*, *Eriocephalus spinescens* and *Ruschia intricata* over the entire experimental period, summer months or winter months

	All months	Summer	Winter
Number of observations	76	45	27
Soil moisture (cm ³ cm ⁻³)	-36.60 (18.84)	131.65* (63.16)	-291.46* (105.52)
Temperature (°C)	-0.49** (0.1738)	0.62 (63.16)	-1.51 (1.11)
Soil Moisture (cm ³ cm ⁻³) :	3.43* (1.14)	-5.17 (3.33)	26.21* (10.10)
Temperature (°C)	6.12* (2.82)	-15.58 (9.29)	20.42 (11.62)
Intercept			
R^2	0.2397	0.5452	0.6566
Adjusted R^2	0.2078	0.5142	0.6170

* $p < 0.05$

Table 4: Linear regression results, with SE in parentheses, for variables predicting monthly changes in average stem length (cm) per plot over the entire experimental period, summer months and winter months for the three most abundant shrub species in the experiment

	<i>Eriocephalus ericoides</i>			<i>Eriocephalus spinescens</i>			<i>Ruschia intricata</i>		
	All	Summer	Winter	All	Summer	Winter	All	Summer	Winter
No. Observations	76	45	27	76	45	27	76	45	27
Soil moisture	-54.9 (28.18)	158.8 (92.85)	-486.7* (172.86)	10.2* (4.71)	21.4*** (4.70)	-11.6 (6.63)	-34.2 (21.05)	29.4*** (7.16)	-14.9* (6.65)
Temperature	-0.8** (0.26)	0.69 (0.73)	-2.9 (0.13)	-0.02 (0.05)	-0.36 (0.13)	1.1*** (0.22)	-4.3* (0.19)	0.1 (0.20)	1.0*** (0.22)
Soil moisture:	5.1** (1.70)	-5.9 (4.90)	44.2* (16.92)				3.2* (1.27)		
Temperature	9.8* (4.22)	-18.8 (13.65)	37.1 (19.85)	-0.4 (1.00)	4.05 (2.30)	-8.25** (2.20)	5.2 (3.15)	-5.2 (3.48)	-7.2** (2.20)
Intercept									
R^2	0.2242	0.5217	0.5915	0.0708	0.3760	0.5383	0.1880	0.3138	0.4712
Adjusted R^2	0.1928	0.4891	0.5444	0.0408	0.3423	0.4963	0.1551	0.2833	0.4320

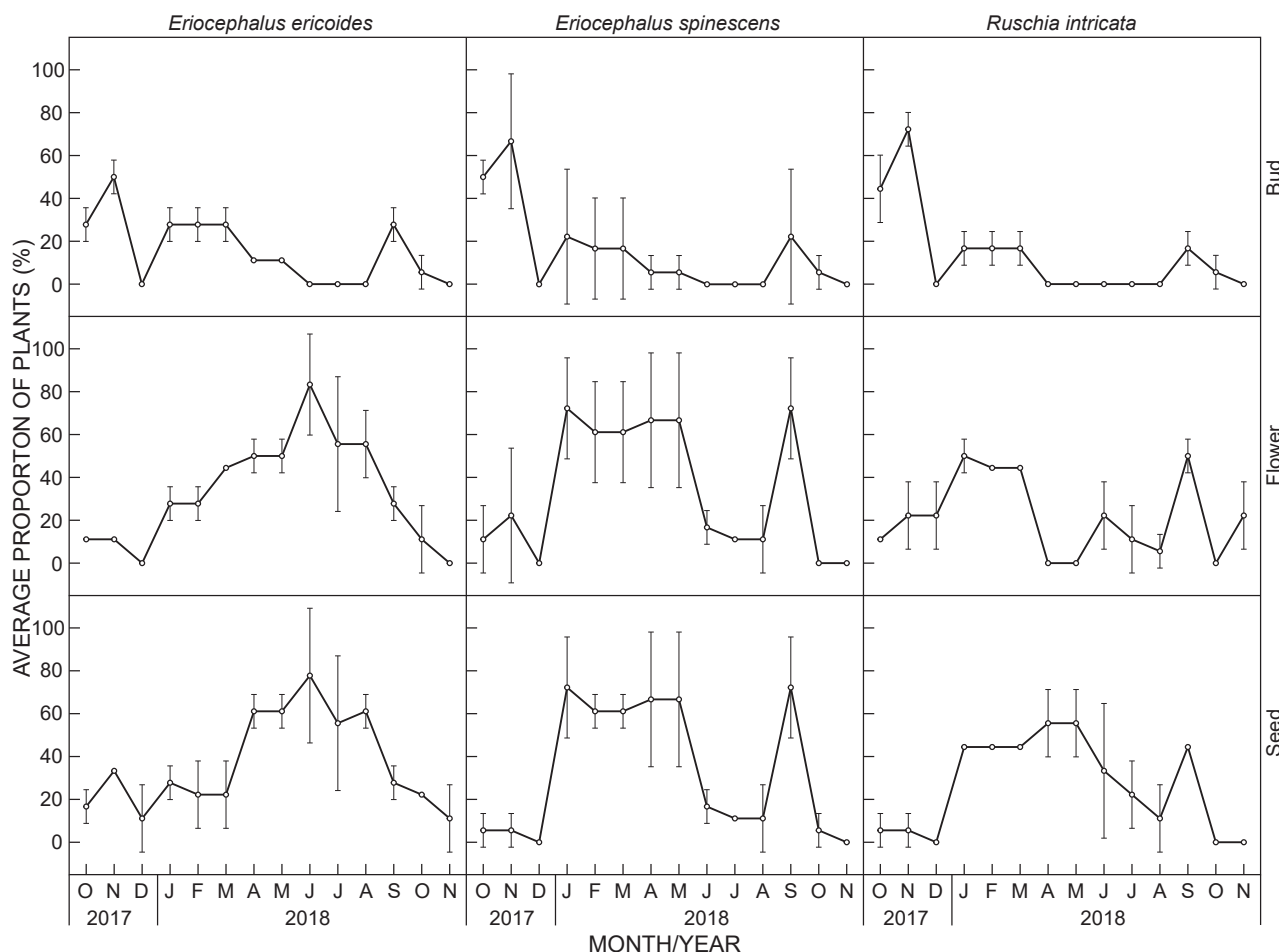


Figure 8: The average proportion ($\pm$ SD; $n = 27$) of plants in the three most abundant species with flower buds, seeds and flowers over the experimental period

taller growth and generally shallower, more extensive root systems, enable grasses to out-compete dwarf shrubs for both light and moisture. We show that shrubs responded strongly to soil moisture, but shrub growth was not lower in the presence of grasses. Furthermore, shrub growth was not higher in areas where competition for light and water were decreased through the removal of above-ground grass biomass. Since the rainfall experienced during the winter period of the experiment was well below average, we were unable to assess the growth of shrubs in response to winter rainfall. Our finding therefore cannot be examined in the context of the hypothesis that shrubs benefit from winter precipitation enabling them to recruit, grow and outcompete grasses (Roux 1966). Our findings show that shrub growth is promoted by an increase in soil moisture after rain regardless of the seasonal timing of rainfall. Seasonality of rainfall is likely to be more important to grasses than shrubs as their growth is restricted by temperature whilst most karoo shrubs are frost tolerant and grow throughout the year (Roux and Vorster 1983; Stock et al. 1993).

Weekly grass clipping severely stunted grass growth and little clipping was needed from the eighth week onwards.

Since grass clipping began in October, after some spring rain, grass was clipped whilst in a growing state resulting in significantly reduced aboveground grass biomass before the onset of the wet summer season in December. This effectively eliminated aboveground competition during the period of the experiment when the most rainfall was received, and shrub growth took place. The severe reduction in grass cover is likely to have resulted in increased soil surface temperature which can affect water infiltration and soil moisture (Moore 1941; Ogden et al. 1997). Since we did not measure soil moisture in each treatment these effects could not be measured. The experiment failed to demonstrate that the reduction of competition by grasses, ostensibly increasing light availability and water availability, results in comparably better growth or reproductive activity of karoo shrubs. Instead, we demonstrated growth responses of shrubs to soil moisture regardless of experimental treatment.

Shrub canopy cover and stem growth

Variation in precipitation can conspicuously impact vegetation through changes in phenology and productivity (Woodward et al. 2004). There was no overall change

in shrub canopy cover or stem length over the fourteen-month experimental period, a pattern that was expected in the control treatment of vegetation dominated by adult plants of a slow-growing nature (Wiegand et al. 2000). This pattern can be attributed to the opportunistic nature of shrub growth in the Nama-Karoo. The fluctuation in shrub growth, represented by change in canopy cover in response to soil moisture, suggests that seasonal rainfall maintains canopy cover, but once mature, does not affect annual increase in height in one year. Many Karoo shrubs can shed their leaves in response to drought and regrow foliage in response to rainfall, regardless of the time of the year (Cowling and Roux 1987). Shrub response to increases in soil moisture is consistent with the pulse-reserve model (Reynolds et al. 2004). Shrub canopy cover responded to increases in soil moisture after rainfall and decreased during dry periods although the degree of response was not equal across species or among individuals of a single species. Stem growth, or the presence of leaves on stems, was dependent on soil moisture and temperature. Cold temperatures limited stem growth, which only occurred when soil moisture increased, and the average daily temperatures were higher. There was a small degree of variation in deciduousness between individuals of the same species. It has been suggested that high growth rates at high soil water content are found to be accompanied by low water-use efficiency, which can afford a species a competitive advantage over others in a community (Midgley and Moll 1993). This has been observed for *E. ericoides* and several other Karoo shrub species (Venter 1995).

Seasonal patterns of growth provide insight into how temperatures influence shrub growth. Temperature stress has been widely studied in the northern hemisphere, but research is lacking in the southern hemisphere where water stress can limit plant growth during the wet and the dry seasons. Seasonality of rainfall is likely to be more important to grasses than shrubs because grass growth is conspicuously restricted by temperature, whilst most karoo shrubs are frost tolerant and grow throughout the year (Roux and Vorster 1983; Stock et al. 1993). *Ruschia intricata* shrubs in the experiment were deciduous, and most plants lost their leaves during the winter months. Edwardes (2018) observed increased growth of *E. ericoides* under artificially increased temperatures, particularly during the summer months. This pattern was attributed to an increase in soil moisture during summer. Since average daily temperature had no significant effect on shrubs when considered over the full 14-month experimental period and during warm months, but low cold season temperatures significantly affected shrub stem growth with some shrubs exhibiting seasonal deciduousness. It appears that cold stress in Karoo shrubs plays a larger role in their seasonal growth than heat stress during the warm season. High variability in the number of individuals that displayed deciduousness might be attributed to plant age or plant health, and we would expect this to affect plant phenology at certain times of the year (Esler 1999).

Shrub phenology, soil moisture and temperature

Reproductive activity for the three most common shrubs in the experiment fluctuated over time. Flowering and seeding were closely associated, and the proportion of *E. ericoides*,

E. spinescens and *R. intricata* flowering and seeding over time was higher than expected suggesting that these species may have more flexible life-history strategies than previously thought (Milton et al. 1999; Riginos et al. 2005). Seed set was closely related to average daily temperature, consistent with observations that flowering phenology and pollinator visitation are both regulated by temperature in the Nama-Karoo (Esler 1999). A larger proportion of plants set seed during summer months, which may be attributed to the presence of pollinators during the warmer summer months. Flowering phenology in the Nama-Karoo has been related to pollinator frequency, which is also regulated by temperature, in particular bee species that are widespread pollinators of Karoo dwarf shrubs (Esler 1999). An understanding of the demography of long-lived species is difficult to achieve in a time-constrained experiment. Often demographic episodes in arid environments are episodic, recruitment only occurs in good years (Carrick 2003). Furthermore, seed production is often separated from germination and emergence seasonally, and possibly annually in semi-arid shrublands (Salguero-Gómez et al. 2012). We did not observe recruitment in experimental plots, suggesting that even during years with wet season rainfall and temperatures that resemble those of an average year, shrubs often do not recruit, even in the absence of competition from grasses. Leaf budding was not in response to increases in soil moisture, but there does appear to be a seasonal cue in the form of change in temperature or photoperiod. There was a similar pattern of stem growth in response to the photoperiod and not soil moisture (Adole et al. 2019).

Implications for land managers

Heavy and indiscriminate continuous grass removal in the Nama-Karoo over a relatively short period of time has serious implications for vegetation cover and grass species composition. Heavy grass removal over a short period of time as simulated in this experiment caused the loss of large palatable tufted grasses that will reduce the grazing potential and carrying capacity of a rangeland. Our findings show that the growth, canopy cover and phenology of Karoo shrubs is highly influenced by both rainfall and temperature. Understanding when shrubs grow and reproduce may be beneficial to land managers and allow them to adapt their grazing strategies in response to rainfall events and seasons. Allowing shrub-dominated rangelands to rest during the wet season will allow an accumulation of biomass which might provide much-needed forage for livestock during dry periods. Furthermore, reducing grazing pressure during wet warm months may facilitate recruitment of some shrub species.

Livestock were excluded from the experiment but could play an important role in competitive interactions between species and growth forms (Wiegand et al. 2000; Aarssen and Keogh 2002). Grazing affects the demography of shrubs (Milton 1992), and palatable individuals would be at a competitive disadvantage. If the reverse were true and grass is preferred by herbivores, as might occur during summer or on a rangeland grazed by exclusively cattle, we would expect that shrubs would have a competitive advantage over grasses under the appropriate climatic conditions.

Conclusion

Measuring growth over a single growing season represents a plant's growth over a small fraction of a Karoo shrub's lifespan and the lifespan of perennial grass competitors (Aarssen and Keogh 2002), particularly in the Karoo where rainfall variation year-on-year is high (du Toit 2017). We propose that competitive interactions between grasses and shrubs may occur under conditions different to, or at different shrub life stages, compared to those experienced over the duration of this experiment, or that competitive interactions between shrubs and grasses are not an important process influencing the state of Nama-Karoo vegetation. Karoo shrubs may be influenced by other prevailing environmental drivers such as rainfall and herbivory. Observations over a longer period may yield more telling results about these interactions, as might observation of how recruitment and establishment of both grasses and shrubs occur in relation to soil moisture, both in the presence and absence of competition from the other growth form.

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CHAPTER 5

Discussion and conclusion

In this thesis I investigated how animal type and stocking rate affect Karoo shrub composition and structure at two sites in the Eastern Upper Karoo (Chapter 2), how fire, as a novel disturbance, affects Karoo shrub communities to drive state change (Chapter 3), and how competition, soil moisture and temperature influence the growth and phenology of Karoo dwarf shrubs (Chapter 4).

This chapter begins with succinct answers to the four main research questions addressed in this thesis. This is followed by a section describing an ideal fodder flow for a land manager in the variable environment of the Nama-Karoo. A general discussion of the findings of Chapters 1, 2 and 3 are presented, with statements on how these findings can be incorporated into Karoo rangeland management. The potential for these findings to contribute to the state-and-transition model for the Eastern Upper Karoo (Milton and Hoffman, 1994) is presented. And lastly, a the way forward for research on Karoo shrubs is discussed.

Research questions

Question 1: How do livestock type and stocking rate, alone or when interacting, impact Karoo shrub communities in the Eastern Upper Karoo?

Answer to Question 1: Animal type and stocking rate affected both the community composition and the structure of Karoo shrubs, though these effects differed between sites. It was clear at both sites that grazing with dorper sheep at high stocking rates negatively impacted both the composition and structure of shrub communities. At both sites heavy grazing by dorper sheep resulted in a degraded rangeland dominated by a small number of undesirable, unpalatable species. Grazing treatment effects were detectable following ten years of rest, demonstrating a pronounced legacy effect of grazing on Karoo rangelands.

Question 2: How does fire affect Karoo shrub communities under varying grazing intensities across a rainfall gradient?

Answer to question 2: Fire markedly changed the composition and structure of Karoo shrublands, although the nature and the extent of the change depended on climate and grazing regime at each site. Immediately following a fire, the above-ground biomass of shrubs was reduced to zero. Thereafter, vegetation cover was made up almost completely by grasses, both perennial grasses that resprout and annual grasses that germinate (though grasses were not studied in any detail, I include this statement to clarify that the burnt area did not remain denuded over time.) Over time, the shrubs that were not killed by fire (the resprouters, which include most species of shrub) coppiced and grew, and returned vegetation composition to a mixture of grasses and shrubs. The few shrub species that were totally killed by fire recruited slowly over time. These fire-intolerant species were often dominant prior to a fire, meaning that their loss following a fire results in a drastically changed shrub community with an altered community structure.

Question 3: Does reduced competition from grasses benefit Karoo shrubs?

Answer to question 3: Karoo shrubs growing in plots where grasses were clipped regularly did not grow faster or respond differently to changes in soil moisture compared to shrubs growing in plots where grass remained unclipped. No competitive effect of grasses was observed.

Question 4: How do soil moisture and temperature influence Karoo shrub phenology and growth?

Answer to question 4: Soil moisture and temperature both influenced shrub growth and phenology. Shrubs grew in response to increases in soil moisture, while temperature determined the rate at which shrubs grew. During the winter months low temperatures slowed growth, and during warm summer months growth rates increased. Flowering occurred for most of the year but seed-set was limited to hot, wet summer months.

Fodder flow in the Nama-Karoo

During a “normal” year when approximately average rainfall is received in the Nama-Karoo, the region experiences a cold dry winter, followed by spring rains that boost shrub growth, which in turn is followed by summer rains that allow grasses, particularly perennial grasses, to grow. Some late summer and autumn rain can be expected and rainfall is the most reliable during the month of March (du Toit, 2022). The build-up of grass and shrub biomass during spring and summer provides fodder for livestock during that time and into the autumn and winter. Most shrubs are able to grow in the cooler temperatures of autumn and this contributes to shrub forage into the winter (Roux, 1966; Roux and Vorster, 1983).

Large variations in rainfall can have severe effects on fodder flow and how land managers manage livestock on Karoo rangelands. An early summer drought delays the onset of plant growth and fodder production in the Nama-Karoo (Anon, 1983), and drastic decreases in the availability of forage affects the growth of livestock and the quality of animal products such as wool, notably “tender wool”, which greatly reduces the economic value of wool (Olivier and Olivier, 2005). A late onset of summer rains can lead to severe removal of grass biomass opening gaps for large flushes of the highly undesirable *Aristida congesta* and *Aristida adscensionis* species. These short-lived grasses provide little forage and can damage wool (Bedford and Roberts, 1975). Reductions in the abundance and size of Karoo shrubs, particularly palatable shrubs, are likely to reduce forage availability, particularly during autumn, winter, and spring.

Vegetation change in the Nama-karoo

Vegetation changes in the Nama-Karoo are driven by grazing in extensive pastoral and wildlife ranching systems, climate (du Toit, 2017; du Toit and O'Connor, 2020; Milton and Hoffman, 1994) and fire (du Toit et al., 2015a). Before the large scale introduction of livestock into the Nama-Karoo, rainfall was the most important determinant of Karoo shrubland structure and composition (Van den Berg et al., 2019), influenced intermittently by locust and caterpillar swarms or migrating ungulates (Rutherford et al., 2006). The introduction of windmills and fences from the late 1800s onward led to a drastic change in how livestock were managed, leading to an increase in stocking rates reaching ten times those

recommended today (Dean and Macdonald, 1994;Archer, 2000). High stocking rates with drought or periods of high rainfall emerged as an important driver of vegetation change in the Nama-Karoo (Kraaij and Milton, 2006; O'Connor and Roux, 1995). More recently, with the increase of grass cover in the Nama-Karoo owing to an extended period of above-average rainfall, the role of fire as a driver of vegetation change has been explored (du Toit et al., 2015b, 2015a).

Milton and Hoffman (1994) addressed the drivers of state change in Nama-Karoo vegetation in a state-and-transition model (Milton and Hoffman, 1994). The model describes directional changes in the abundance of either palatable or unpalatable Karoo shrubs and grass with changing rainfall, grazing intensity, season of rainfall and grazing, and larger climatic events such as droughts or long periods of high rainfall. The model does not consider livestock type or animal type in its description of how grazing drives state change nor does it address how fire affects Karoo shrub communities. Furthermore the effects of each driver on the structure of shrub communities or phenology of individual Karoo shrub species is not considered. The inclusion of fire into a state-and-transition model for the Eastern Upper Karoo is vital since the abundance of grass in the region has increased in correspondence with increasing rainfall over the past 60 years (Arena et al., 2023;du Toit and O'Connor, 2014; Masubelele et al., 2014). Changes driven by climate or grazing are slow compared with an instant, drastic vegetation change resulting from a fire in a fire-naïve system. Accounting for these differences in a state-and-transition model is important for a better understanding of vegetation change in the Eastern Upper Karoo. Despite the lack of evidence revealed in this study of a competitive effect of grasses on shrubs, further study of this interaction may be warranted as grass abundance increases.

Grazing management in the Eastern Upper Karoo

Differences in the legacy of grazing management between different sites shows that the long term impact of grazing management decisions by land managers should be examined on a site-by-site basis. Similarly, management recommendations should be given with these differences in mind. Most Karoo landscapes are not homogenous and most Karoo farms have variation in topography, soil type and soil depth, and hence vegetation composition and productivity. Grassier areas with deep soils and fewer species should be considered more sensitive than areas with shallow, rocky soils and a diverse community of small statured

shrubs. The resilience of rocky, steep communities has not been explored, though their ability to resist drought has been documented after periods of drought (Myburg, 1994; Anon, 1983, Milton et al., 1995). Furthermore, Anon (1983) recommended that land managers move livestock into “koppie” (rocky hills) paddocks of their farms during wet summers to allow shrub communities in flatter terrain of sandy soils to recover from grazing during the dry season.

During years of ‘normal’ (non-drought or extremely wet) rainfall, the most important driver of vegetation change in the Karoo is grazing (du Toit and O’Connor, 2020; O’Connor and Roux, 1995). Stocking rate and animal type influence the composition of Karoo shrub communities (Chapter 2). Changes in community composition and structure of Karoo shrub communities were evident many years after the withdrawal of livestock from a grazing system and this legacy effect is important as it will determine how fast, or slowly, the state of Karoo vegetation will change. Despite ten years of rest during which average rainfall was received, there were clearly detectable differences of the effect of grazing treatments at both sites of the Afrikaner-Hereford grazing trial between the removal of livestock from the trial and this study. Studies have indicated that the removal of livestock does not necessarily induce recovery, even at the scale of several decades (Seymour et al., 2010). Van der Merwe and Milton, (2019) applied the Wiegand and Milton (2016) simulation model to a Karoo site where they described how Karoo shrub demography remained unchanged due to their slow growth. They described the legacy of historic grazing regimes as demographic inertia. Similarly, Esler, (1999) attributed the legacy effect in Karoo communities to the slow growth and intermittent recruitment of Karoo shrubs. A collapse in the shrub population would decrease forage availability and carrying capacity of the rangeland would drop drastically.

In general plant communities growing on rocky soils are more resilient to disturbance than communities growing in sandy soils (Wonkka et al., 2016). Degradation of Karoo rangelands caused by grazing primarily affects plant population demography after which productivity and diversity decline (Kraaij and Milton, 2006). The impact of stocking rate and animal type at the Afrikaner-Hereford grazing trial was more profound on the rangeland with deep sandy soils compared to those with shallow rocky soils. Rockier, more diverse shrublands that were characterised by a Karoo shrub community and composed of small-statured Karoo shrubs were affected by grazing to a lesser degree than the less diverse Karoo shrub communities on deep sandy soils. In the Succulent Karoo, soil type is an important determinant of community

composition and site productivity (Esler and Cowling, 1993). The extent to which this is true is not known for the grassier Eastern Upper Karoo, but it can be assumed that the soil-vegetation relationship is an important determinant for how a rangeland responds to grazing (Esler and Cowling, 1993).

Compositional changes that are driven by grazing can have a profound effect on the grazing capacity of a rangeland (Vorster, 1999). The impact of grazing on the composition and structure of Karoo communities is highly dependent on the type of livestock and the rates at which they are stocked. Grazing by dorper sheep had a dramatic effect on Karoo shrub communities, particularly when stocked at high stocking rates. This is attributed to the non-selective grazing behaviour of dorper sheep. Dorper sheep are less selective grazers and tend to spend more time at an individual shrub compared to merino sheep (Brand, 2000). A consequence of this is that there is an increased chance that a higher proportion of the growing regions of the plants are removed during grazing by dorper sheep compared to merino sheep. A depletion in leaf and stem biomass reduces the reproductive output of individual plants reducing the number of flowers and seeds produced (Wiegand et al., 1995). The failure to recruit may result in the loss of that species from a community, as was observed in the heavily grazed dorper treatments at the Afrikaner site described in Chapter 2.

A noteworthy change in Karoo shrub species composition at the Afrikaner site was the high abundance of the highly undesirable *Senecio* sp. and *Hertia pallens* with other common shrubs such as *Selago geniculata* absent. The legacy of long term heavy stocking by dorper sheep was the eradication of nearly all shrubs other than some unpalatable species, and the remaining vegetation was predominantly annual, short-lived, or unpalatable perennial grass species (unpublished data, M. van Lingen, Grootfontein Agricultural Development Institute). The effect of grazing by merino sheep on the composition and structure of Karoo rangelands was more varied and highly dependent on stocking rate. Additionally these effects were more severe on rangelands with deep sandy soils dominated by larger statured shrubs such as *Eriocephalus ericoides*, *Pteronia tricephala* and *Pteronia sordida*.

The rate at which dorper and merino sheep are stocked influenced the cover of palatable and unpalatable shrubs on Karoo rangelands. At higher stocking rates, the cover of palatable dwarf shrubs decreased. This effect was more profound when grazed by dorper sheep compared to merino sheep. In contrast, the cover of unpalatable species was higher on

heavily stocked rangelands. With heavy stocking, the overall palatability of the rangeland decreases over time, reducing the carrying capacity of the rangeland. Unfortunately the legacy of that grazing which resulted in a rangeland with significantly reduced palatable dwarf shrubs means that even after long periods of rest the rangeland does not always recover to its former state. An important future avenue of research should be to investigate whether managerial interventions, other than rest, might hasten the recovery of degraded Karoo rangelands. Examples of this might be the introduction of different types of animals after varying periods of rest, the season when introduction of livestock are reintroduced or reseeding or replanting areas with palatable shrub species.

Karoo shrublands on shallow rocky soils were more resistant to structural changes driven by grazing treatment at the Afrikaner – Hereford grazing trial. Similar patterns have been observed during periods of drought in arid regions. Milton et al (1995) found higher mortality of karoo shrubs in deep sandy soils compared to rocky areas on the landscape after a drought near Steytlerville. this pattern is attributed to lower rates of evaporation from the soil underneath rocks and stones (McAuliffe and Hamerlynck, 2010). Although communities were changed by heavy grazing by dorper sheep neither animal type nor stocking rate had a lasting detectable effect on the structure of Karoo shrubs or functional types in Karoo shrub communities in shallow rocky soils. Three Karoo shrub species, *Rosenia humilis*, *Eriocephalus ericoides* and *Ruschia intricata* were extirpated by heavy grazing by dorper sheep. *Ruschia intricata* is considered important during periods of drought when it provides forage to sheep which generally avoid it during times of normal rainfall.

Novel management considerations

Since Karoo shrub communities respond differently to stocking rate and animal type, the texture and depth of the soil, together with the Karoo shrub community, should be taken in to account by graziers when determining which rangelands to stock and how to manage different areas within their property. Such managerial decisions must be made with the consideration of other factors that limit shrub communities such as fire.

The true history of fire in the Nama-Karoo is not known but evidence suggests that fires on flat landscapes were not a regular occurrence. Climate determines incidence and frequency of fire in the Nama-Karoo because the abundance of grass increases during years of high rainfall

(Masubelele et al., 2014), thereby increasing flammable biomass which can carry a fire across a Nama-Karoo shrubland. The likelihood of fire during drier years is lower as fire would not travel across the landscape due to the sparsity of grass resulting in gaps between shrubs (Cheney and Sullivan, 2008).

Mean annual rainfall over the eastern Nama-Karoo has increased by 15% since the 1950s. This, together with a significant decrease in stocking rate has resulted in an increase in grass cover over the last 60 years (Arena et al., 2023, Masubelele et al., 2014, 2015). This pattern of change is consistent with already-recognised effects of rainfall and grazing on vegetation dynamics in the eastern Upper Karoo (du Toit et al., 2018; Masubelele et al., 2014; O'Connor and Roux, 1995). Given predicted shifts in vegetation, particularly biome shifts, we need to consider the direct effects of novel fires on the community composition and structure of Karoo shrublands (Arena et al., 2023).

Disturbance from grazing and climate shifts may take years to induce a significant effect on Karoo dwarf shrub communities (Chapter 2), whereas fire induces a sudden pronounced change in Karoo vegetation by removing all plant biomass and causing the extirpation of some (often dominant) shrub species (Chapter 3). Grasses are first to regrow after a fire resulting in a complete state change into a grass-dominated system. Shrubs start to resprout after the first rainy season after the fire, so this period is likely critical in the recovery of Karoo rangelands following fire. Land managers should avoid grazing these areas during this period to allow shrubs to recover and prevent further limitations on shrub structure from grazing (Chapter 2).

The degree of change in a shrub community as a result of fire is largely determined by rainfall and there is a clear effect of fire on Karoo rangelands along a wide west to east geographic area and rainfall gradient. Compositional differences are more conspicuous between burnt and unburnt rangelands in areas that have a higher mean average rainfall. The greater compositional change after a fire in the eastern reaches of the Eastern Upper Karoo is attributed to the higher proportional cover of Karoo shrub species that are killed by fire. Once these species are extirpated by fire they do not re-enter the system quickly and may take up to 40 years to recolonise (du Toit et al., 2015a). One reason for this may be that shrub seedlings are palatable and cannot withstand being grazed. Land managers across the East to West rainfall gradient should adapt rest periods after a fire accordingly. In the wetter eastern areas

heavy grazing in previously burnt areas will limit the recruitment of fire-intolerant seeding species that dominated the community before the fire. Adapting grazing management to rest burnt areas to allow shrubs the opportunity to flower and seed in summer (Chapter 4) will promote entry of seeds into the system. Lenient grazing thereafter might provide seedlings a chance to grow and then persist in the ecosystem. Grazing with sheep would likely be more damaging to Karoo shrubs than cattle so land managers should consider grazing these areas with cattle instead of sheep. Sheep graze selectively removing sensitive growing regions of karoo shrubs (Bedford et al 1975) whereas cattle are less likely to select shrubs in the presence of grass.

Most Karoo shrub species are fire-tolerant, and can resprout after a fire. Only a few species are fire-intolerant non-sprouters. These individuals are killed by fire and can only return to a rangeland through successful germination of seeds and recruitment of seedlings. However, fire-intolerant seeding species such as *Eriocephalus ericoides*, *Eriocephalus spinescens* and *Ruschia intricata* are often the most abundant species in a community. These species contributed on average 22% of shrub cover at the studied fire sites (Chapter 3). The loss of these fire-intolerant species was the largest contributor to vegetation change after a fire. Since fire-intolerant species are often dominant in a community and are larger in stature than other Karoo shrubs, their loss results in a post-fire community which is quite different in composition and structure than before the fire, and offers vastly different temporal grazing opportunities to livestock. The replacement of these individuals by other Karoo shrubs is slow. Initially grass fills the gaps, thereafter smaller fire-tolerant shrubs dominate the communities resulting in a new vegetation state in the months after the fire (du Toit et al., 2015a).

Changes in vegetation structure affect ecosystem functioning and land use. The cover and density of fire tolerant species depends on rainfall and grazing management both before and after the fire. A comparison of Karoo shrub functional types across the west to east gradient of the Eastern Upper Karoo showed that burning tended to change the composition, cover and density of Karoo shrub functional types. In town commonages, heavy continuous grazing eliminated most palatable shrub species resulting in a community dominated by unpalatable fire-tolerant species which experienced little change as a result of a fire. If fires reoccur in these communal rangelands they will become increasingly uniform and degraded as heavy continuous grazing and fire act together leaving a shrub community dominated by small

statured unpalatable dwarf shrubs. By contrast, rangelands stocked leniently, under rotational grazing and rest after the fire, resulted in diverse shrublands consisting of many functional types.

The Richmond site (Chapter 3) was an anomaly amongst the burnt sites examined. This site has not been grazed to any significant degree since the establishment of the railway, over 100 years ago, which separates it from the adjacent commercial farming rangeland. At this site shrubs were larger than their conspecifics at the other sites, and there were some fire-intolerant species present in the burnt area. This suggests that in the absence of grazing, fire-intolerant seeders are able to return to a rangeland but only after a very long period of time, one that exceeds the rest period after fires in the other rangelands in this study. Unfortunately very long periods of rest for burnt areas is impracticable for commercial graziers and communal graziers grazing their cattle on commonages.

The effect of fire on Karoo shrub communities has important implications for fodder flow and rangeland management. Karoo shrubs provide a stable source of fodder for livestock over the whole year, other than perhaps during summer months when some species lose their leaves in dry conditions. Furthermore, Karoo shrubs are able to survive long dry periods during which grasses senesce and become dormant, or even die. Changes in species composition or the loss of Karoo shrubs after a fire causes an immediate loss of grazing which may recover to a significantly less palatable community over time.

Climate change predictions (Engelbrecht et al., 2009) show an increase in rainfall in the Eastern Upper Karoo, which is likely to result in both increased grass abundance and consequently a higher frequency of fires. The implication of more fires in the Eastern Upper Karoo would be the reduction of shrub cover which in turn, at least initially, will likely result in higher grass cover, which through a positive-feedback process subsequently increases the likelihood of a repeat fire. The implications for shrubs from repeat fire is unknown and the period of rest between fires would determine the long-term effects of such an event. Land managers will be required to adapt their farming practises to manage these risks and effects from fire appropriately. After a fire land managers will need to adapt their management to allow burnt areas to rest. Thereafter land managers should graze burnt areas during the wet season when grass is plentiful and allow shrubs to recover by resting during spring and autumn. To prevent grazing of shrubs land managers should graze these areas with cattle

where possible. Additionally land managers should graze with merino sheep rather than dorper sheep to avoid the heavy indiscriminate nature in which dorper sheep graze and thereby giving shrubs a better opportunity to recover.

Land managers may also need to adapt their management in order to reduce the risk of fires, including repeat-fires. To identify the risk of fire, land managers should monitor grass fuel loads, grass curing (i.e. senescence), and current weather conditions. They would also need to recognise farming activities that pose novel ignition risks, for example sparks from angle grinders, tractors or welders, or ash and smouldering debris discarded on rubbish heaps which have been shown to ignite fires in the Karoo (du Toit et al., 2015a). To prevent ignitions alongside main roads, land managers should maintain firebreaks along the fence lines. Land managers can further adapt their grazing management to graze boundary camps heavily to prevent the build-up of grass to reduce fuel loads, and this may be especially useful after receiving good spring rains.

This study found that there is a profound legacy effect of fire across the Eastern Upper Karoo. Although burnt communities tended towards their pre-burnt states they were still 60% dissimilar to adjacent unburnt vegetation after 10 years. The period required for full recovery, or the return to a rangeland that resembles its pre-burnt state is unknown, though likely less than 40 years in the Eastern Upper Karoo (du Toit et al., 2015a). Therefore, the inclusion of fire into an updated state-and-transition model for the Eastern Upper Karoo is essential for modelling how Eastern Upper Karoo rangelands will change after a fire, an instant transformer, while interacting with grazing and a changing climate which act more slowly to change vegetation states.

As rainfall in the Eastern Karoo increases (du Toit and O'Connor, 2014; Harmse et al., 2021) and with long term increases in rainfall predicted (Engelbrecht et al., 2009), the eastward expansion of the Grassland Biome into the Nama-Karoo has been predicted (Arena et al., 2023). A direct impact of a higher grass abundance is competition between plants and shrubs, especially in a the semi-arid environment of the Karoo where rainfall is sporadic and soil moisture is an overriding determinant of community structure. For this reason the models which explain competition between woody plants and grasses are based on water availability. During summer, rainfall occurs usually in the form of thunder showers, while during cooler months frontal rain is more common. Accurate measurement of soil moisture enables the

direct comparison of plant growth to the amount of available moisture eliminating unmeasured loss of rainfall to run off and evaporation from the soil surface.

In a field trial, regular clipping killed large tufted palatable grasses (Chapter 4). Although clipping cannot be directly equated with grazing, the finding suggests that heavy continuous grazing over a relatively short period can have deadly consequences for Karoo grasses. The loss of large tufted grasses would reduce the amount of fodder available and have severe implications for fodder management, especially for cattle farming in the Karoo. The absence of grass did not facilitate shrub recruitment and no seed germination took place in the absence of shrubs or grasses. This may be because grasses facilitate shrub recruitment by creating a favourable microclimate and maintain soil moisture by shading the soil, or that shrub seeds require conditions not experienced over the period of the experiment to recruit.

Grasses showed no competitive effect on adult shrubs in the clipping trial (Chapter 3) and competitive interactions between adults or seedlings of shrubs and grasses were not observed. Although this interaction was not examined in the field experiment described in Chapter 3 the removal of shrubs by fire (Chapter 4) resulted in an increase in grass cover (du Toit et al. 2015a). The proliferation of grasses after a fire indicates that adult shrubs prevent grass germination and establishment. The removal or extensive damage to shrubs as a result of animal trampling. Similarly, when shrubs were trampled during high density kraaling (corralled), the number and richness of both succulent and non-succulent shrubs decreased, whereas the number and richness of grasses increased (McManus et al., 2018)

A pre-emptive strategy of maximising root depth may give shrubs a competitive advantage over grasses as roots of Karoo shrubs can extend several metres into the soil in addition to their ability to develop vast shallow root systems (Esler, 1999; Casper and Jackson, 1997). Competitive interactions between different life stages of growth forms within communities were not described in Chapter 4. The absence of shrub seedling establishment in the clipped and control plots suggests that grasses did not prevent shrub seedling establishment in the experimental period. Despite this; grass competition is likely to be more severe on shrub seedlings after a germination event compared to competition on adult shrubs due to their small size and underdeveloped roots (Esler, 1999).

In the absence of grazing, Karoo shrubs grow, flower, bud and produce seed in response to rainfall (Chapter 4). This growth is dependent on temperature. While most Karoo shrubs grow throughout the year and are frost tolerant (Stock et al., 1993), temperature stress during very cold periods restricts a plant's potential response to soil moisture. *Ruschia intricata* is deciduous with most plants losing their leaves during winter. High soil moisture and warm temperatures in summer promote faster growth. During winter months Karoo shrub growth in response to an increase in soil moisture is slower than the response to an increase in soil moisture in the warm summer months. Resting rangelands after rain during the wet season will allow for a greater accumulation of shrub biomass, and this may be an effective way to accumulate forage for an approaching drier winter season or for longer dry periods.

A large proportion of the common shrubs *Eriocephalus ericoides*, *Ruschia intricata* and *Eriocephalus spinescens* flower and seed throughout the year, suggesting that these species have a more flexible life strategy than previously thought. Seed-set was closely related to average daily temperature, consistent with observations that flowering phenology and pollinator visitation are both regulated by temperature in the Nama-Karoo (Esler, 1999). A larger proportion of plants set seed during summer months, which may be attributed to the presence of pollinators during the warmer summer months. Flowering phenology appears to be closely related to pollinator frequency, which is also regulated by temperature. This is true for bee species that are widespread pollinators of Karoo dwarf shrubs (Esler 1999). There appears to be a separation between seeding and recruitment for *Eriocephalus ericoides*, *Ruschia intricata* and *Eriocephalus spinescens*. Although these species produce seed, recruitment of Karoo shrubs is seldom observed, even during periods of average rainfall. The time that seeds remain viable in the soil has not been studied but it appears that there is a seasonal, annual or possibly longer, separation between seed production and germination, indicating that the seeds of these species may possess some form of dormancy. Henrici (1935) described the high variation in the dormancy of karoo shrub seeds being between a matter of days to two years.

Understanding when shrubs grow and reproduce may be beneficial to land managers and allow them to adapt their grazing strategies in response to rainfall events and seasons. Allowing shrub-dominated rangelands to rest during the wet season will allow an accumulation of biomass which might provide much-needed forage for livestock during dry

periods. Furthermore, reducing stocking rate during wet warm months may facilitate recruitment of some shrub species.

Contributing to an updated state-and-transition model for the Eastern Upper Karoo

Milton and Hoffman (1994), presented a state-and-transition model for the Eastern Upper Karoo. In their model they describe how grazing and rainfall drive the transition of Karoo rangelands between states. The findings presented in this thesis have been used to make contributions to the model with suggestions on how the model can be updated in the future. Descriptions on transitions between states are described according to Figure 1 (figure 4 in Milton and Hoffman (1994)), and a proposal for additional states and transitions follows.

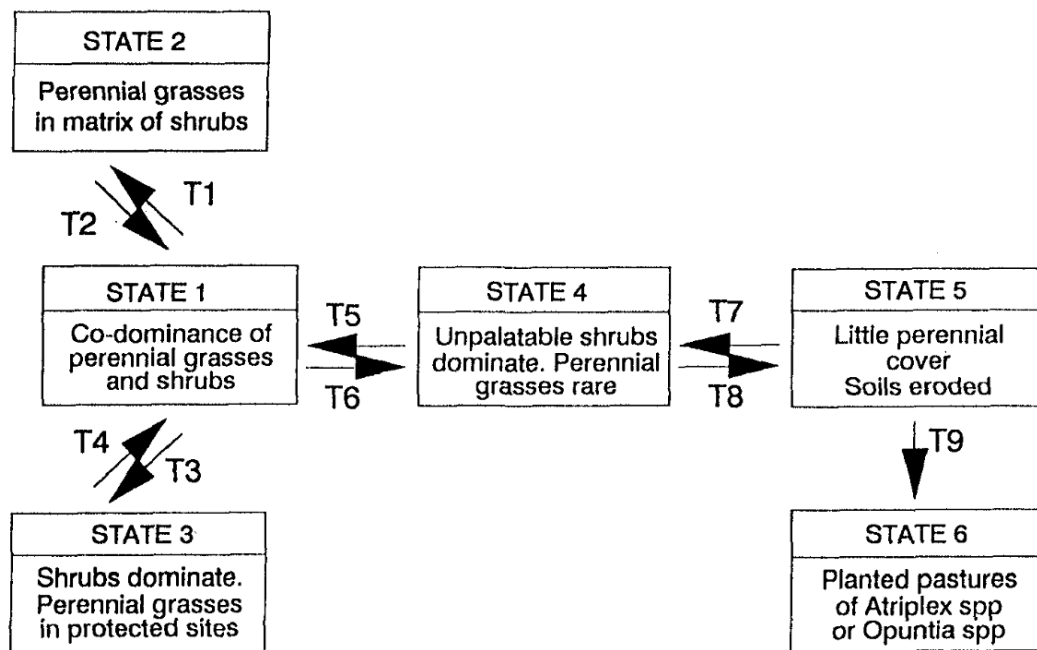


Figure 1: Milton and Hoffman, (1994) Figure 4: State-and-transition model for the grassy eastern Karoo (Acocks' Veld Type 36, False Upper Karoo).

State 1 - State 2

State 1 is a karoo rangeland where the plant community consists of karoo shrubs and grasses. The description of this State does not take into account variability in shrub composition and structure across karoo landscapes. Aside from naming several specific shrub species (*Pentzia incana*, *Plinthus karooicus*, *Pteronia* spp., *Rhigozum obovatum*, *Rosenia humilis*), no

mention is made of the palatability or functional groups that make up the shrub component. Since shrub communities vary across a landscape according to soil type and topography (Chapter 2) the inclusion of a description of functional types would be useful as these could be compared across many areas. Furthermore, the very common shrubs *Eriocephalus ericoides*, *Eriocephalus spinescens*, *Pentzia globosa* and *Ruschia intricata* are not included in the description of state 1 (Chapter 2). State 1 is most likely made up of large-statured palatable and unpalatable karoo dwarf shrubs, with a low abundance of smaller palatable dwarf shrubs as these are likely to be selected when an area is lightly grazed (Chapter 2). Light summer grazing with good summer rainfall (T1) will transform State 1 to State 2. This transition would be very slow and would require more than 10 years of rest (Chapter 2). State 2 is a more desirable state as a result of high summer rainfall resulting in the dominance of perennial grasses. Grazing and good rainfall would ensure all species present had an opportunity to become larger in stature and more dense. The shrub component has not received further description but it is likely that the shrub community making up State 2 is more diverse than that of State 1, with a higher abundance of sensitive species such as *Selago geniculata* and *Delosperma* sp. (Chapter 2). The transition to State 1 (T2) can be driven by rotational grazing at recommended stocking rates, but it will depend on animal type. Dorper sheep will have a more noticeable impact on the shrub component compared to merino sheep and highly palatable species will be selected over time which will decrease their cover and density. Grazing stress during summer will impact the phenology of shrubs and may reduce their reproductive output, such that, over a long period of time these species may be lost from the community driving the transition back to State 1 (T2).

State 1-State 3

State 3 is dominated by Karoo shrubs, the palatability of which is dependent on management. Perennial grasses are only found present in protected areas as a result of summer drought. The transition from State 1 to State 3 (T3) is driven by summer grazing at recommended stocking rates. Shrubs are able to respond to significant rainfall events by flowering and seeding but grazing during summer will reduce the reproductive potential of karoo shrubs as this is when most seeds are produced (Chapter 4). It is also unknown whether germination takes place after these rainfall events, even in the absence of grass (Chapter 4). It is unknown, but considered unlikely, that significant germination events will lead to successful

recruitment in the presence of grazers even at recommended stocking rates (Chapter 2, Chapter 4) as the conditions required for Karoo shrub recruitment are not known. Under rotational grazing, palatable shrubs in State 3 will decrease over time, this effect will be larger if grazed by dorper sheep (Chapter 2) even when summer rainfall returns (T4). The return to a State 1 after good summer rainfall might be a state composed of different functional types with increased grass abundance. Management will determine the composition and structure of State 3. The density of unpalatable karoo shrubs increases and the density of palatable dwarf shrubs decreases after long term rotational grazing (Chapter 2).

State 1-State 4

State 4 is a highly undesirable state, and is a result of continuous selective grazing and drought (T6) which has resulted in a community dominated by unpalatable, toxic, spiny shrubs and annual grasses. This state can also be achieved with rotational grazing at high stocking rates with both dorper and merino sheep (Chapter 2). Undesirable unpalatable *Senecio* spp., and *Pteronia* spp. are common in these areas (Chapter 2). Seasonal removal of the reproductive organs of the shrubs interferes with phenological processes and together with constant removal of leaf matter, plant cover and density are significantly reduced until individuals are lost from the community. Flowers and seeds are not produced and no germination takes place leading to a collapse in the shrub component. If seeds can enter the system seedlings are grazed. The transition from the degraded State 4 to State 1 would require a very long period of rest, of more than 10 years (Chapter 2) before grazing is reintroduced. Furthermore, it is unlikely that the recovery of a shrub community through the introduction of seed from less degraded areas would readily occur in a period shorter than ten years (Chapter 2, Chapter 3).

State 4 - State 5

State 5 is a highly degraded state caused by overgrazing. State 5 was not encountered in this study. Even the town commonages which were continuously and chronically grazed supported a composition of shrubs and annual grasses, albeit that the shrubs were undesirable unpalatable species. It is noteworthy that the extreme levels of grazing pressure investigated in this study did not result in a transition to State 5 (Chapter 3). The transition from State 4 to State 5 would occur because of severe soil erosion.

State 6

This state was not considered in this thesis.

New states and transitions

The inclusion of additional states and transitions would strengthen the model. State 7 is proposed as a result of a fire after a period of high rainfall. State 7 is a grass-dominated community with few shrubs (Figure 2). Transition to State 7 could be from States 1 (T10), 2 (T12), 3 (T14) or 4 (T16). The return from State 7 (T11, T13, T15 and T17) would occur in the shortest period of time in the absence of grazing (Chapter 3) under conditions of above-average rainfall, and slowly under heavy continuous grazing. Time and intensity of grazing, rainfall conditions and the previous state will determine whether State 7 transitions back to its former state or to another described state. Livestock type should be included. Grazing by sheep, particularly dorper sheep, would slow the transition (Chapter 2) back to States 1, 2, 3 and 4. In all these transitions, fire-tolerant sprouting species would recover quite quickly but fire-intolerant seeders could take up to 40 years to recover (Chapter 3). Heavy continuous grazing with drought may result in a transition to State 5 as resprouters would not be able to grow and germination from seed would be prevented under prolonged dry conditions (Chapter 3).

State 7 – State 1

State 7 is a community that has been transformed by fire to a grass dominated state, the shrub component of this state is dominated by resprouting shrub species. State 1 is a karoo rangeland where the plant community consists of karoo shrubs and grasses. The transition from State 7 to State 1 (T11) could occur after a period of prolonged rest and a delayed reintroduction of livestock (Chapter 3). Rest would allow resprouting species to regrow to their pre-fire size and allow non-sprouting seeder species to establish in the community (Chapter 4). In this transition fire intolerant species including *Eriocephalus ericoides*, *Eriocephalus spinescens* and *Ruschia intricata*, formerly dominant species, should have an opportunity to return to the community (Chapter 4). Rainfall would play an important role in the time taken for this transition to take place. Periods of high rainfall would quicken this transition.

State 7 – State 2

State 2 is a desirable state dominated by perennial grasses and a diverse shrub community. The transition from State 7 to State 2 (T13) would be highly dependent on rainfall. High rainfall would benefit all species present by giving them an opportunity to become larger in stature and become more dense. High rainfall favours large tufted perennial grasses (Arena et al., 2023). The shrub component is likely to have a higher diversity of shrubs compared to State 7. In the absence of heavy and continuous grazing the abundance of sensitive species such as *Selago geniculata* and *Delosperma* sp. will increase and other resprouting species will establish resulting in a diverse shrub community.

State 7 – State 3

The transition from State 7 to State 3 (T15) is highly dependent on management. State 3 is a shrub dominated community with perennial grasses growing in protected areas. The palatability of plants in State 3 is dependent on management and the perennial grasses are only found present in protected areas as a result of summer drought. If animals are introduced after a fire and heavy or continuous grazing takes place the community in State 3 will be dominated by unpalatable shrubs but if grazing is managed at recommended or below recommended stocking rates the shrub community in State 3 might be more diverse with a range of growth forms of palatable and unpalatable species. Low summer rainfall restricts the abundance of grasses.

State 7 – State 4

The transition from State 7 to State 3 (T17) might occur when livestock are reintroduced into a previously burnt and rested rangeland at high stocking rates, and/or grazed continuously. Under high grazing pressure palatable species and perennial grasses would be grazed heavily and unable to persist in the community (Chapter 3). Palatable fire intolerant seeder species would not be able to recruit under heavy grazing (Chapter 4) and palatable resprouter species would be grazed upon heavily rendering them unable to recruit. Animal type would influence the rate at which the transition took place and the change from State 7 to State 4 would be accelerated by grazing by dorper sheep (Chapter 2).

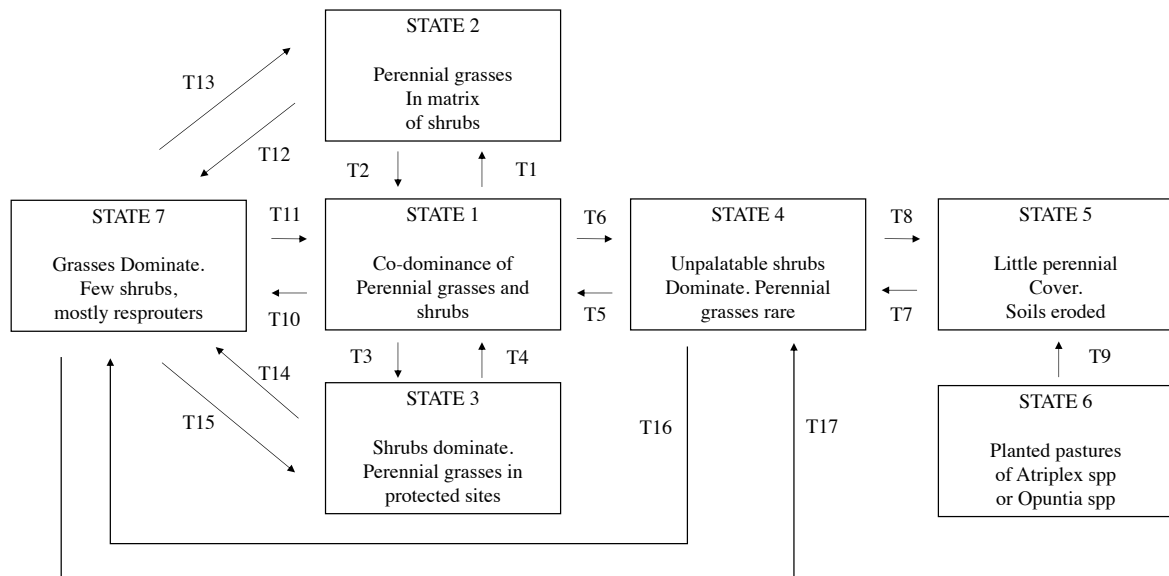


Figure 2: Modified state-and-transition model for the Eastern Upper Karoo showing a new state and transitions.

Conclusion

From this study we can make several conclusions on the effects of fire, grazing, grass-shrub and competition on the composition and structure of karoo shrub communities. It is clear that there is a strong legacy effect of grazing by livestock on Karoo rangelands and, following grazing-induced compositional changes, shrub communities do not return to a ‘normal’ state in the medium-term, even under conditions of rest from grazing and good rainfall.

Furthermore, different sheep breeds impact shrub communities in different ways. In this study it was shown that dorper sheep, when stocked at high stocking rates, can have near-catastrophic effects on shrub communities, extirpating most shrubs other than some unpalatable (and probably toxic) species. The impacts of merino sheep were less severe, but significant nonetheless. Importantly, the effects of different breeds of animals at different stocking rates were not consistent across sites. The primary difference between the two sites that were studied was their soil properties: deep soils that were largely rock-free, and shallow, rocky soils. As soil chemistry was similar at the sites, no characteristics should limit shrub growth, furthermore soil chemistry did not emerge as important variable determining vegetation composition, it appears that the soils’ physical properties are potential drivers, with soil water availability hypothesised to be of greatest importance. The role that soil

physical properties play in determining vegetation characteristics, and how it influences resilience, is conspicuously under-researched in the Nama-Karoo. Stating it simply, without an improved understanding of the influence of soils, any formulation of a theory of the response of Karoo vegetation to external drivers, or indeed of management recommendations for land managers, is unlikely to succeed.

It was clear that fire has severe effects on shrub populations in the short term, where all shrubs are either killed or top-killed (i.e. aboveground material is killed, but the plant resprouts). The nature of vegetation recovery after the fire is related to the ratio of shrubs that were not killed (i.e. resprouters) to shrubs that were killed (i.e. non-sprouters). In turn, these are related to average rainfall, because non-sprouters tend to be dominant in higher-rainfall regions. Accordingly, in the western, lower-rainfall regions, vegetation tended to recover faster because many of the shrubs were resprouters and began regrowing shortly after the fire. The influence of grazing by livestock was also important. At very low stocking rates, shrubs flourish following fire, and non-sprouters re-colonise the area relatively quickly. Under conditions of 'normal' stocking rates, recovery takes place but non-sprouters are slow to re-colonise. Under heavy, continuous grazing the effects of fire appear limited because vegetation can return to its pre-burnt condition relatively quickly. This is because the only shrubs that are present in such systems are unpalatable sprouters which manage to re-grow despite the presence of high livestock numbers. The study clearly shows that shrub recovery following burning is universally slow, but fastest when stocking rates are close to zero. Accordingly, from an ecological perspective, post-fire management recommendations should be based on prolonged destocking regimens. However, such an approach is economically not feasible for land managers. Future research should investigate how to balance the ecological requirements of burnt veld with management and economical needs of land managers. Management interventions that promote the consumption of grass (which resprouts rapidly following fire) by livestock, and reduce the consumption of shrubs, would presumably be useful. Practically, this may translate into stocking with animals which prefer grass (e.g. cattle), are less damaging to shrubs (e.g. merino rather than dorper sheep), or grazing at times of the year when the protein content of grasses is sufficiently high to render shrubs less attractive to livestock, and thereby to have minimal impact on shrub recruitment.

The issue of repeat fires at a site was not explored in this study, though it is expected to be of importance. Positive feedback loops between grass and fire are well known and documented

in other vegetation types, and their basic mechanistic theory would suggest that the same may occur in the Karoo. Should it emerge that repeat fires do occur, and do so increasingly owing to the positive feedback nature of such events, it is predicted that there Nama-Karoo rangelands would shift to semi-arid grasslands. This would be of considerable importance in sheep farming enterprises because shrubs contribute meaningfully to forage at times of the year when grass availability is low, which in reality comprises the cooler half of the year.

Despite competition between plants being a nearly universal occurrence, this study demonstrated that grasses had little or no competitive effect on the growth and phenology of adult shrubs. One explanation is that this one-year trial reflected competition under only very limited environmental conditions. Another explanation may be that the two growth forms access water from different soil strata, which again highlights the importance of considering soil physical properties when investigating vegetation dynamics in the Karoo. Shrub growth, with or without grasses in the vicinity, is strongly correlated to rainfall, but this is modified by temperature. Shrubs grew after rains all year round, but highest growth rates were when temperatures were highest. This is contrary to the notions that only grasses grow during the hottest months, and that shrub growth is highest in the spring and autumn seasons when temperatures are moderate. This finding is important for managers of livestock production enterprises, and also of importance in understanding shrub recovery following fire. Shrub flowering is also dependent on rainfall and took place throughout the year. However, seeding occurred mainly during the warm season. The roles of temperature on seed-set, as well as the availability of pollinators at different times, are two obvious avenues for future exploration.

It is very clear that numerous factors influence the growth, phenology and size of Karoo shrubs and their community composition. It is also very clear that these responses are not spatially uniform, and a major gap in our knowledge is the role of edaphic conditions on shrub growth and demography.

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