THE EFFECT OF HIGH-DENSITY, SHORT-DURATION STOCKING ON SOILS AND VEGETATION OF MESIC GRASSLAND IN SOUTH AFRICA

By

SINDISO CHARLOTTE CHAMANE

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PREFACE

The research contained in this dissertation was completed by the candidate while based in the Discipline of Grassland Science, School of Life Sciences of the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg campus, South Africa, under the supervision of Professor Kevin Kirkman, Mr Craig Morris and Professor Tim O'Connor. The research was financially supported by the National Research Foundation-Thuthuka PhD Track grant, Professor Kevin Kirkman, School of Life Sciences and the College of Agriculture, Engineering and Science of the University of KwaZulu-Natal.

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

Signed: _________________________

S.C. Chamane (Candidate)

Date:

Signed: _________________________

Professor Kevin P. Kirkman (supervisor)

Date:

DECLARATION 1: PLAGIARISM

I, Sindiso Charlotte Chamane, declare that:

(i) the research reported in this dissertation, except where otherwise indicated or acknowledged, is my original work;

(ii) this dissertation has not been submitted in full or in part for any degree or examination to any other university;

(iii) this dissertation does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons;

(iv) this dissertation does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:

a) their words have been re-written but the general information attributed to them has been referenced;

b) where their exact words have been used, their writing has been placed inside quotation marks, and referenced;

(v) where I have used material for which publications followed, I have indicated in detail my role in the work;

(vi) this dissertation is primarily a collection of material, prepared by myself, published as journal articles or presented as a poster and oral presentations at conferences. In some cases, additional material has been included;

(vii) this dissertation does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the dissertation and in the References sections.

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Signed: Sindiso C Chamane

Date:

DECLARATION 2: PUBLICATIONS

For the three chapters (Chapter 3 – 5) submitted, chapter 3 and 4 are published and chapter 5 is intended for submission as a paper to an appropriate scientific journal. My three supervisors have been included as co-authors because of their significant scientific input. The conferences at which this work has been presented at are also shown below.

Chapter 3

1. Chamane SC, Kirkman KP, Morris C and O'Connor TG. 2015. The effect of high density livestock grazing on a mesic grassland in South Africa. Poster presentation at the 50th Annual Grassland Society of Southern Africa, Royal Agricultural Showgrounds, Pietermaritzburg, KwaZulu-Natal, South Africa, 19th to 23rd July 2015.

2. Chamane SC, Kirkman KP, Morris C and O'Connor TG. 2016. Effects of short duration, high density stocking on soil properties and plant species composition of a mesic grassland in South Africa. Poster presentation at the 10th International Rangeland Congress, Teacher's Credit Union Place, Saskatoon, Saskatchewan, Canada, 16th to 22nd July 2016.

3. Chamane SC, Kirkman KP, Morris C and O'Connor TG. 2016. The effect of high density livestock grazing on a mesic grassland in South Africa. Platform presentation at the 1st International Long-Term Ecological Research Open Meeting, Skukuza, Kruger National Park, South Africa, 9th to 13th October 2016.

4. Chamane SC, Kirkman KP, Morris C and O'Connor TG. 2017. What is the long-term effect of high density, short duration stocking on the soils and vegetation of mesic grassland in South Africa? *African Journal of Range and Forage Science* 34: 111-121.

Chapter 4

5. Chamane SC, Kirkman KP, Morris C and O'Connor TG. 2014. A study of the impact of short duration, high density stocking on plant diversity in South African mesic grasslands. Platform presentation at the 49th Annual Grassland Society of Southern Africa, Phillip Sanders, Bloemfontein, Free State, South Africa, 20th to 25th July 2014.

6. Chamane SC, Kirkman KP, Morris C and O'Connor TG. 2014. Can forbs survive holistic grazing? Platform presentation at the 5th Annual Diamond Route Research Conference, Multipurpose Rooms, Cornerstone Building, De Beers Corporate Headquarters, Johannesburg, South Africa, 21st to 22nd October 2014.

7. Chamane SC*, Kirkman KP, Morris C and O'Connor TG. 2017. Does high density stocking affect perennial forbs in mesic grassland. *African Journal of Range and Forage Science* 34: 133-142.

Chapter 5

8. Chamane SC*, Kirkman KP, Morris C and O'Connor 2017. Response of three perennial forb species to intensive defoliation and interspecific competition in mesic grassland.

In all cases, I have been responsible for planning the experimental protocol, collecting and analysing the data, interpreting the findings and writing the papers. My supervisors have given statistical advice and read successive manuscripts of the various chapters, making suggestions for improvement based on their areas of specialized knowledge. In chapter 3, one of the presentations was judged the best student presentation at the at the 10th International Rangeland Congress, Teacher's Credit Union Place, Saskatoon, Saskatchewan, Canada, 16th to 22nd July 2016. The award was by the Australian Rangeland Society (ARS). The papers in chapter 3 and 4 were invited for a special edition on Holistic Resource Management (HRM) in the *African Journal of Range and Forage Science*.

Signed: Sindiso Charlotte Chamane

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ABSTRACT

High-density, short-duration stocking (HDG) is currently gaining popularity amongst farmers in South African mesic grasslands but little is known about its potential impact on soil properties and plant species composition, particularly the forbs (herbaceous dicotyledonous and non-graminoid monocotyledon) which contribute more to plant diversity than grasses. Under HDG, animals are stocked at higher stocking rates and densities than conventional grazing systems and burning is discouraged. This study used a fence-line contrast approach to compare the long-term impact of "real world" HDG systems with rotational grazing systems at a lower stocking density (LDG) on soils and vegetation composition including forb growth habits at two study sites, Kokstad and Cedarville. An experimental trial was set up at Ukulinga Research Farm to determine the short-term effects of HDG compared with no grazing on plant species composition and demography of the selected perennial forbs. Another field experiment was used to determine the response of three mesic grassland perennial forb species (*Afroaster hispida, Gerbera ambigua* and *Hypoxis hemerocallidea)* to intense defoliation and interspecific competition with a grass species (*Themeda triandra*). Soils were more compacted under HDG but soil chemical properties did not differ between HDG and LDG at both Kokstad and Cedarville. There was a low percentage cover of desirable palatable grasses and high forb species turnover under HDG at Kokstad and low grass and forb species responses at Cedarville. There was high litter accumulation under HDG over the long- and short-term period. High litter accumulation reduces irradiance for plants, and may lead to lower basal cover. The intense grazing and trampling due to the higher stocking rate and stocking density under HDG resulted in less erect forb growth habits and more prostrate growth habits at Kokstad. A study of demography revealed that HDG threatened future populations of the grazing-sensitive species *Afroaster hispida, Agathisanthemum chlorophyllum* and *Gerbera ambigua* through increased mortality or reduction in the recruitment of large from small individuals. Intense defoliation altered the competitive response of *A. hispida*, it had a high competitive response when undefoliated but when defoliated its competitive response was reduced. *Gerbera ambigua* and *H. hemerocallidea* were not affected by the interaction between defoliation and competition. Findings from this study has shown that HDG potentially has a negative impact on soil health and vegetation composition of South African mesic grassland.

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CHAPTER 1: INTRODUCTION

1.1 Rationale for the research

Historically, grassland management in South Africa has been largely aimed at the sustainable production of livestock. Extensive rangeland research focused on grass composition because it constitutes most of the forage for livestock production and the forb (non-graminoid monocotyledon and herbaceous cotyledon) composition has been largely ignored (Tainton 1999). However, it is forbs rather than grasses that constitute most of the plant diversity in grasslands (Bullock et al. 2001, Morris 2004). High plant diversity is important for maintaining ecosystem stability and productivity (Tilman and Downing 1994). If there are more species they are more likely to overlap in their functional characteristics and there is a greater probability that an ecosystem will be capable of coping with a disturbance. Although the importance of plant diversity in grasslands has been realised in ecosystem terms, particularly the forb diversity (Uys 2006, O'Connor et al. 2010, O'Connor et al. 2011), factors determining their richness, abundance of individual species, and composition in response to different grazing management practices are simply not known.

Commercial livestock production, particularly cattle, predominates in the mesic grasslands because of the high stable rainfall which results in high forage production (Palmer and Ainslie 2005). Grazing management systems commonly used by commercial farmers in South African mesic grasslands include variations of the flexible stocking rotational grazing with at least one paddock rested for a full season on a rotational basis (Venter and Drewes 1969, Kirkman and Moore 1995). These conventional rotational grazing systems apply moderate stocking rates and stocking densities and fire is regularly used to remove excessive litter and moribund material (Kirkman and Moore 1995). However, over the past decades an extreme form of rotational grazing i.e. high-density, short-duration stocking (HDG) has been gaining popularity amongst the mesic grassland farmers due to the contended benefits that include increased stocking rate that result in greater profit compared to other grazing systems (Zietsman 2010, Phillips 2014). HDG uses multi-paddocks to concentrate a large number of animals in small areas for short durations and the rest period is advocated to be longer compared to conventional rotational grazing systems (Savory 1983, Savory and Butterfield 2016). Under HDG soil health is postulated to be improved by breaking the soil crust through hoof action to alleviate compaction, and by increasing nutrient availability through an increased rate of nutrient cycling from standing dead herbage to soils and from high concentrations of dung and urine in paddocks (Joseph et al. 2002, Savory and Butterfield 2016). Concentrated large herds of livestock, rather than fire, are advocated as a tool to remove standing dead herbage at the end the dry period, and litter is allowed to accumulate for protecting soil moisture (Savory and Butterfield 2016). HDG is also contended to improve plant diversity and the productivity of the preferred foraging grass species (Johnson 2012). There is however no empirical evidence in support of these claims for mesic grasslands in South Africa, particularly the forb component which contributes most to plant diversity in grasslands.

1.2 Aims

The aim of this study was to determine the impact of high-density, short-duration stocking (HDG) on soil properties; plant species composition and vegetation dynamics with the main focus on the forbs, in a South African mesic grassland.

1.3 Objectives

- To determine the long-term effects of ‘real’ world HDG systems compared with conventional rotational grazing systems at lower density stocking (LDG) on soil properties and vegetation composition including forb growth habits at two study sites, Kokstad and Cedarville using a fence-line contrast approach,
- To determine the short-term effects of HDG compared with no grazing on plant species composition and demography of the selected perennial forbs using a field experiment, and
- To determine the response of three mesic grassland perennial forb species to intense defoliation and interspecific competition in a field experiment.

1.4 References

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1.5 Outline of dissertation/thesis structure

Chapter 1 is the general introduction with aims and objectives of the thesis. Chapter 2 comprises the literature review, providing a detailed motivation and rationale for this study. Chapter 3 – 5 are the results chapters. Each of the results chapters is self-contained, comprising an introduction, materials and methods, results and discussion, and conclusions. Chapter 6 is the final chapter, providing general discussion and conclusions as well as future research possibilities. Below is a brief outline of what each of the results chapters focused on:

Chapter 3 focuses on the long term (> 15 years) effects of high density, short duration stocking (HDG) on soil physical and chemical properties; vegetation structure; plant species composition and diversity including the forb growth habits. It used a fence-line approach to compare ‘real world’ grazing systems i.e. HDG vs conventional rotational grazing systems at lower stocking rate and stocking density.

In Chapter 4, the short-term effects (2 – 3 years) of high density, short duration stocking compared to no grazing were assessed on vegetation structure, plant species composition and diversity, and the demography of the selected perennial forb species.

Chapter 5 assessed the response of three mesic grassland perennial forb species to intense defoliation and interspecific competition.

CHAPTER 2: LITERATURE REVIEW

2.1 Introduction

Natural grasslands are economically and ecologically important in South Africa. They occupy about 29% of the country but less than 2% is under conservation management in protected areas, thus biodiversity in the natural grasslands is under threat due to mismanagement such as over grazing (Reyers and Tosh 2003, O'Connor and Kuyler 2009). Acquisition of additional land as protected areas is a challenge due to the increasing land-use demands (O'Connor and Kuyler 2009). As an alternative, a strategy of mainstreaming biodiversity conservation within other land use sectors was proposed and promoted (Pierce 2002). Commercial livestock production systems have been identified as a suitable land-use to mainstream biodiversity conservation (O'Connor and Kuyler 2009). However the major challenge with this, is that not much is known about how other species, apart from grasses, respond to various livestock management systems. Grasses contribute most to biomass in grasslands but it is the forbs (herbaceous dicotyledon and non-graminoid monocotyledon) that constitute most to species diversity (Bullock et al. 2001). High plant diversity maintains ecosystem functioning and the delivery of services such as forage and habitat for wildlife, mitigate draughts and floods, and provide aesthetic beauty (Isbell et al. 2011, Oehri et al. 2017).

Commercial livestock production systems on natural grasslands predominates in the mesic grasslands (Palmer and Ainslie 2005). Mesic grasslands receive relatively high, greater than 600 mm annual rainfall and as a result forage quantity for livestock is high (Tainton 1999). However forage quality is low in the non-growing season, particularly on the acidic sandy loam soils which have a low nutrient status derived from shales, mudstones and sandstones (Ellery et al. 1995). Different grazing systems apply various management tools such as conservative stocking rates and fire to maintain grassland condition and improve forage quality (Kirkman and Moore 1995). An extreme form of rotational grazing, high-density, short-duration stocking (HDG) that advocates the replacement of fire with high density grazing has been gaining popularity in the mesic grasslands (Savory 1983, Zietsman 2010). Some of the advocated HDG benefits include high stocking rates and stocking densities that will increase nutrient cycling from the high concentration of animals dunging and urinating resulting in improved forage quality and more profits (Zietsman 2012).

The aim of this review was to determine the potential impact of high-density, short-duration stocking compared with other commonly used grazing systems on plant diversity, focusing on the forbs because they make up most of the diversity on South African mesic grasslands. The objectives of this review was to first discuss some of the determinants of plant species composition in South African grasslands with the key focus on mesic grasslands, then review common grazing systems including HDG on mesic grasslands and lastly identify potential HDG impacts on factors that affect growing conditions of plants (soils and vegetation dynamics); plant species composition (grasses and forbs) and forb population dynamics.

2.2 South African grasslands

The grassland biome is centrally located in South Africa and is dominated by the hemicryptophytes of Poaceae (Bredenkamp 1999). It is shaped by a range of environmental conditions such as rainfall, temperature and altitude and covers a range of soil types from humic clays to poorly structured sands (O'Connor and Bredenkamp 1997). Natural grasslands are an important reservoir of plant diversity (Palmer and Ainslie 2005). At 1000 m^2 scale, South African grasslands on average are richer than the Fynbos biome and the Kwongan of Australia (Cowling et al. 1991). Although the structure of grasslands is relatively uniform, there is a wide variation in the floristic composition, functional attributes of plant species, vegetation dynamics as determined by environmental variables such as mean annual precipitation, temperature and soil type (O'Connor and Bredenkamp 1997), altitudinal gradient (Mucina et al. 2006) and the impact of disturbances such as fire and grazing (Bond et al. 2003).

The major division in the grassland biome is determined by the moisture gradient (Mucina et al. 2006). Based on annual rainfall there are two main types of grasslands in South Africa referred to as the fire climax (mesic) and climatic climax (dry) grasslands (Tainton 1999). Mesic grasslands receive high (>600 mm annually) stable rainfall resulting in high forage quantity and as a result livestock production particularly cattle predominates in these grasslands (Palmer and Ainslie 2005). Leaching of the soil nutrients is moderate to high resulting in infertile dystrophic mesic soils (Fynn and O'connor 2005). The degree of leaching is dependent on the soil type (O'Connor and Bredenkamp 1997). Leaching is quite high for the sandy soils and they are infertile hence forage quality drops in the non-growing season when plants are mature whereas for the clay-rich soils leaching is moderate to low and they are fertile thus forage quality is relatively high throughout the year (Mucina et al. 2006). Mesic grasslands are dependent on fire to maintain them as grasslands, in the absence of fire they can turn into a savanna or forest, hence they are referred to as fire climax grasslands (Tainton 1999, Briggs et al. 2005, Bond and Parr 2010). The dry grasslands receive low (<600 mm annually) erratic rainfall resulting in low forage quantity (Ellery et al. 1995). The soils are less leached and they are fertile or eutrophic hence forage quality is high throughout the year (O'Connor and Bredenkamp 1997). The dry grasslands are referred to as climatic climax grasslands because even in the absence of fire they remain as grasslands. One of the explanations is that dry grasslands are either too arid or too cool to permit woody species (Tainton 1999). This study focuses on mesic grasslands where cattle production predominates hence dry grasslands will not be discussed further in this review.

2.2.1 Mesic grasslands

South African mesic grasslands provide essential ecosystem services such as high quantity forage for livestock, conservation of soil and water provision (Reyers and Tosh 2003, Blignaut and Aronson 2008). In the catchment areas, they stabilise soils and promote rainfall infiltration (Bosch and Hewlett 1982, Le Maître et al. 2002, Blignaut et al. 2010). However, the majority of the natural mesic grasslands has already been lost due to irreversible land use changes such as built environment, dams and mines or transformed by crop and timber production (Jewitt et al. 2015). Most of the remaining natural mesic grasslands are under livestock production, particularly cattle (Palmer and Ainslie 2005). The best way to conserve plant diversity in mesic grasslands would be to mainstream it under the livestock production systems. Hence, it is important to understand how various grazing management systems affect plant diversity.

Disturbances such as fire and grazing are used as management tools by managers of grazing systems and they affect plant species diversity in various ways (Tainton 1999). More frequent fires favours high plant species diversity (Kirkman et al. 2014, Venter et al. 2017) and if there is grazing it needs to be moderate (Joubert et al. 2017). High grazing pressure due to heavy stocking rates with burning reduces plant species diversity (Scott-Shaw and Morris 2014). The effect of grazing alone with no burning on plant species diversity in South African mesic grasslands is yet to be determined.

Patterns in plant species diversity are also influenced by soil type, infertile soils support greater species richness than fertile soils as explained by Tilman’s (1982) resource availability hypothesis. Limiting resources, such as soil nutrients, create more niches which allow for more ways in which species can coexist (Tilman 1982). The addition of the limiting resource eliminates niche dimensionality, increases competition and as a result reduces the number of species that can coexist (Harpole et al. 2016). The addition of soil nutrients on infertile mesic grasslands reduced plant species richness in South African mesic grasslands (Fynn and O'Connor 2005) and on similar grasslands in North America (Gough et al. 2000) and Britain (Stevens et al. 2004, Maskell et al. 2010). Hence, South African mesic grasslands on infertile soils potentially support more plant diversity than mesic grasslands on fertile soils. This is further justified by the historical distribution of herbivores as elaborated below.

Mesic grasslands on fertile soils are highly productive, they produce forage of high quality from the nutrient rich soils and forage quantity is high due to high rainfall (Hempson et al. 2015). Plant diversity in fertile mesic grasslands was most likely low due to the high herbivore densities that were likely supported since forage quality and quantity was high (Mucina et al. 2006). Mesic grasslands on infertile soils produce forage of low quality in the non-growing season when plants are mature, the grasses have a high ratio of C:N compared to grasses on fertile soils (Ellery et al. 1995). Hence, herbivores that were likely supported by infertile mesic grasslands were bulk grazers because they can tolerate forage of low quality (Hempson et al. 2015). Bulk grazers unlikely occurred in high densities since fires were a frequent occurrence due to high fuel load that would have accumulated as a result of low herbivore densities (Venter et al. 2017). Hence, infertile mesic grasslands supported high plant diversity as a result of low grazing pressure and more frequent fires compared to fertile mesic grasslands which had high grazing pressure and consequently less frequent fires. Currently mesic grasslands on infertile soils support livestock production, possibly at higher densities than what the area historically supported (Little et al. 2015).

2.3 Grazing strategies in mesic grasslands

Grazing management systems were developed as a tool to increase livestock production and they focused on improving the growth of palatable grass species because grasses constitute most of the forage for livestock (Venter and Drewes 1969, Barnes 1992, Kirkman and Moore 1995). Recently, the importance of conserving biodiversity within livestock production systems under various grazing management systems has been realised (O'Connor et al. 2010).

A single main dichotomy for classifying grazing systems is continuous versus rotational (Bell 1950). Continuous grazing systems are systems where no land is put aside for rest but rather all the land is utilised. In this system the only factor that is manipulated is the stocking rate (metabolic biomass of animals per unit area per unit time). Rotational grazing involves manipulation of season, frequency and intensity of grazing using a number of paddocks, period of occupation and periods of absence (Tainton et al. 1999). In South African rangelands, continuous grazing systems were not favoured by scientists, amongst other reasons was the issue of high selective grazing (Booysen 1969, Tainton et al. 1999). Hence, rotational grazing systems were developed based on one of two principles; high utilisation grazing also known as non-selective grazing (HUG) and high performance grazing also known as controlled selective grazing (HPG), to try and solve the issue of selective grazing (Booysen 1969). The two principles applied different methods to solve the issue of selective grazing, high utilisation grazing has relatively long grazing periods of about two weeks, to ensure that animals graze the preferred and non-preferred species (Acocks 1966). The high performance grazing is based on short periods of grazing about a week or less, to ensure the preferred species are moderately grazed to maintain their vigour while the non-preferred species are not grazed leading them to become moribund and die (Booysen 1966).

2.3.1 Conventional rotational grazing systems vs high-density, short-duration stocking

Grazing management systems commonly used by commercial farmers in South African mesic grasslands include variations of the flexible stocking rotational grazing, based on either HUG or HPG principles, and include the use of fire (Venter and Drewes 1969, Kirkman and Moore 1995, Tainton et al. 1999). Over the past decades, an extreme form of rotational grazing, high-density, short-duration grazing (HDG) has become increasingly popular because of the contended benefits which include higher stocking rates, than the conventional rotational systems, resulting in higher profits (Savory 1983, Zietsman 2010, Phillips 2014). Management variables that differ between conventional rotational systems and HDG are discussed below.

2.3.1.1 Stocking rate

Stocking rate is the number of animals expressed as the metabolic mass per unit area of the grazing land, including rested areas, per unit time (Trollope et al. 1990). There are varying opinions on the optimum stocking rate with the HDG proponents recommending up to double the normally recommended stocking rates for the conventional rotational grazing systems (Savory 1983). Optimum stocking rate is the maximum stocking rate that can sustain livestock production and maintain the grassland in good condition (Danckwerts and King 1984). The recommended optimum stocking rate for conventional rotational grazing systems in South African mesic grasslands is determined based on the condition of the grassland often referred to as veld condition (Hardy et al. 1999). A number of factors are used to determine the veld condition of an area and they include species composition, mainly grass species; the vigour of the palatable species; basal cover; soil surface condition; rainfall and topography. Once the condition of the grassland has been determined see Camp and Hardy (1999) for the process, the stocking rate of the area is then determined relative to a benchmark, which is a grassland or veld that should be capable of providing the highest possible sustained animal production (Hardy et al. 1999). Higher stocking rates under conventional grazing systems have been shown to have negative impact on livestock production and veld condition (O'Reagain and Turner 1992).

The HDG systems recommend higher stocking rates (doubling the recommended stocking rate) compared to conventional rotational grazing systems which are said to result in high animal performance (Savory 1983, Zietsman 2012). However, there is no empirical evidence to support sustainability of higher stocking rates in the South African mesic grasslands.

2.3.1.2 Stocking density

Stocking density is the number of animals expressed as the metabolic mass per unit area at any instant in time (Trollope et al. 1990). Based on the concept of ‘a natural grazing system’ where a large number of herbivores are said to bunch together in a group to escape predators, HDG promotes high stocking density compared to conventional rotational grazing systems by concentrating a large number of animals in a small area over a short period of time, for an average of 7 days (Savory 1983, Nordborg 2016). The intense trampling from the high stocking density is said to trample all the standing plant material that is not grazed to achieve uniform defoliation (Savory 1983). The high stocking density under HDG also creates hoof action which is contended to break the soil crust and alleviate compaction; promote seed germination; increase water infiltration and the retention of water in the soil. The high concentration of dung and urine in paddocks as a result of the high stocking density is contended to increase the rate of nutrient cycling (Savory and Butterfield 2016).There is, however, no empirical evidence to support these claims on the mesic grasslands.

2.3.1.3 Rest

Rest is when grazing is deferred in a paddock or camp to allow it to recover (Tainton et al. 1999). Conventional rotational grazing systems generally apply two types of rests, short and long rests (Kirkman and Moore 1995). Short rest also referred to as period of absence are short term rests (ranging around 40 days in mesic grasslands) to allow forage to accumulate for animals (Tainton et al. 1999). Long rests are rotational season- or year-long rests and animals are removed for the benefit of plants (Morris et al. 1992). The chosen season of rest is determined by the desired outcome. For example if the desired outcome is to accumulate leaf material then a spring rest is applied; if the desired outcome is seed production and plant vigour then a summer rest is applied; and if the desired outcome is to store excess carbohydrates for winter then an autumn rest is applied (Kirkman and Moore 1995). A year-long rest achieves all of the listed seasonal outcomes (Tainton et al. 1999).

The HDG system introduced a time controlled approach to grazing and resting, where the period of grazing and the resting period is varied according to the growing conditions of plants (Savory 1983, Savory and Butterfield 2016). HDG systems are advocated to apply longer rest periods compared to conventional grazing systems (Savory and Butterfield 2016). However, unlike the conventional grazing systems which have two rest types, HDG systems have one type of rest which ranges from 60 to 180 days (Savory 1983). The rest under HDG is said to allow vegetation growth and reproduction (Savory and Butterfield 2016), but it does not distinguish between the different seasons yet vegetation growth and reproduction mainly takes place in the growing season.

2.3.1.4 Number of paddocks

A paddock also referred to as a camp is the smallest unit to which grazing management is applied (Trollope et al. 1990). The conventional rotational grazing systems generally have four to eight paddocks whereas the HDG systems have more than eight paddocks (Tainton 1985). For the conventional grazing systems, one or two of the paddocks commonly get rested for a full season- or year-long on a rotational basis incorporating a burn, while the other paddocks are grazed (Danckwerts and Teague 1989, Engelbrecht et al. 2004). For the HDG systems, the high number of paddocks is to ensure that each paddock gets a short intense grazing and a relatively long rest period (Savory and Butterfield 2016). Despite multi-paddocks gaining popularity in the South African mesic grassland, they have not been shown to be superior to fewer paddocks on forage biomass production, plant species diversity, grassland condition and animal performance (Tainton et al. 1977, Gammon 1978, Gammon and Twiddy 1990, Morris and Tainton 1996, Morris and Tainton 2002).

2.3.1.5 The use of fire

Fire is considered essential in maintaining the structure and functioning of mesic grasslands (Morris and Tainton 2002). The absence of fire for more than 4 years, can result in excessive litter accumulation which reduces light availability and suppresses primary production in mesic grasslands (Everson and Everson 2016) and on similar grasslands globally (Knapp et al. 1998). The exclusion of fire for about five decades results in the invasion of woody species (Morris and Tainton 2002). Generally, conventional rotational grazing systems include burning to remove dead moribund material, to improve range condition (in terms of soil cover and forage quality for livestock production) and to control the invasion of woody species (Danckwerts and Teague 1989, Morris and Tainton 2002, Engelbrecht et al. 2004). More frequent burning (every 2 – 4 years, depending on rainfall of the previous season) is recommended for the mesic grasslands because they are highly productive (Trollope 1999). Burning annually is not recommended because it reduces dry matter production (Tainton et al. 1999). It is recommended that all the burning takes place when the grass is dormant and as close as possible to the growing season to ensure the soils are not susceptible to erosion (Trollope and Trollope 2010). To remove moribund material and to improve range condition, the recommended burning season is after the first spring rain, when the grass is still dormant and the fire danger rate is low (Uys et al. 2004). This ensures a cool fire of low intensity which is relatively easy to manage. To control woody invasion, the recommended time of burning is late in winter or early spring before the first rains to ensure a hot intense fire to kill the woody species (Trollope 1999). The HDG systems, discourages the use of fire, rather concentrated large herds of livestock are advocated as a tool to remove standing dead material and the moribund material is allowed to accumulate to protect the soil moisture (Savory 1983, Savory and Butterfield 2016). There is however, no empirical data, on the effects of replacing fire with high density grazing on the structure and functioning of mesic grasslands.

2.4 Impact of grazing systems on soils and vegetation dynamics

2.4.1 Soil physical and chemical properties

Soil properties are important for plant growth and development and for the maintenance of a healthy and stable ecosystem (Weil and Brady 2016). Grazing affects soil chemical and physical properties in various ways which in turn influences vegetation dynamics (Medina-Roldán et al. 2012). Soil nitrogen is a primary limiting nutrient in grasslands (Tilman 1988). Although the increase of soil N in mesic grasslands may result in an increase in primary production (annual net primary production), the abundance of palatable grass species and the forb species richness and diversity may decline (Fynn and O'Connor 2005).

A soil physical property that is mainly influenced by grazing animals through trampling is soil compaction which is the densification of the soil due to the applied stress from trampling (Dunne et al. 2011). Compaction of the soil is dependent on soil texture type, clay soils contain fine particles and can easily be compacted while sandy soils which have coarser particles are not prone to compaction (Donkor et al. 2002). Compaction of the soil negatively affects soil productivity because it reduces infiltration rate and air movement into and through the soil thus reduces the air and water available to plant roots (Donkor et al. 2002). Additionally, reduced infiltration rate increases overland flow resulting in soil erosion and the development of rills (Loch 2000).

The impact of HDG on soil physical and chemical properties has received considerable attention showing conflicting findings with some studies showing that HDG improves the soil properties (Beukes and Cowling 2003, Teague et al. 2011) and others showing that it does not (McCalla et al. 1984, Warren et al. 1986, Dormaar et al. 1989, Dong et al. 2012). The majority of these studies were conducted on small scale experiments and extrapolating their findings to landscape scales have been questioned (Teague et al. 2008, Teague et al. 2013). There are no landscape scale studies that have compared HDG to other rotational grazing systems but rather the landscape scale studies compared HDG with continuous grazing system and the stocking rate was similar in both the grazing systems (Earl and Jones 1996, Jacobo et al. 2006, Teague et al. 2011). The impact of HDG at landscape scale at higher stocking rates compared to other rotational grazing systems on soil physical and chemical properties is yet to be determined.

2.4.2 Litter

Plant litter is the dead plant material on the soil surface which is distinct from standing dead plant material (necromass) (Dyksterhuis and Schmutz 1947). Plant litter is important for increasing water availability through slowing down surface water movement; improving water infiltration; reducing evaporation from the soil surface and buffering soil temperatures against extreme heat and cold (Larson and Whitman 1942, Facelli and Pickett 1991). Litter is also important for nutrient cycling, as decomposed litter returns nutrients back into the soil (Dyksterhuis and Schmutz 1947). The rate of decomposition is depended on litter quality, litter of high quality which has a low C:N ratio decomposes faster compared to litter of low quality with a high C:N ratio (Bot and Benites 2005).

Litter accumulation is dependent on biomass production, areas with high biomass production, as is in the mesic grasslands due to the relatively high stable annual rainfalls, can accumulate excessive litter (Facelli and Pickett 1991). Excessive litter cover can reduce irradiation received by especially low-statured plants (Weaver and Rowland 1952, Foster and Gross 1998), and that may hinder their growth and ultimately result in their mortality (Bews 1925, Carson and Peterson 1990). High litter cover can also inhibit seed germination and emergence of some plant species (Facelli and Pickett 1991) as a consequence of seeds not receiving a sufficient cue and the physical difficulty of a new seedling breaking through dense litter (Foster and Gross 1998). Tiller production of palatable grasses is also reduced under high litter accumulation (Everson et al. 1985). In the mesic grasslands, substantial amounts of litter are expected to accumulate under the HDG system due to the exclusion of fire. This high litter accumulation may potentially have negative effects because mesic grasslands are not moisture limited but instead are highly productive (Palmer and Ainslie 2005) and the litter may be slow to decompose (Heady et al. 1992). In addition, when the excessive litter is ignited, there may be a potential increase in fire temperatures at the soil surface which may be detrimental to the plants (Prior et al. 2016).

2.4.3 Plant species composition

South African mesic grasslands on low nutrient soils historically had low herbivore densities with more frequent fires and supported high plant species diversity and richness compared to other grasslands (Mucina et al. 2006, Hempson et al. 2015). Plant species in this region are likely adapted to the interaction between frequent fires and low to medium grazing (Little et al. 2015). Most conventional rotational grazing systems in the region apply fire and grazing interactively as management tools (Kirkman and Moore 1995). HDG which is an intense grazing system that has been gaining popularity in the region, advocates the replacement of fire with high density grazing (Savory 1983, Savory and Butterfield 2016). The effect of fire and grazing on plant species composition and functional traits will be reviewed below, as well as how conventional rotational grazing systems vs HDG apply these tools. Grasses and forbs will be reviewed separately due to their potential differences in response to fire and grazing (Fynn et al. 2005a).

2.4.3.1 Grasses

Generally grasses require some form of a disturbance (fire and grazing), which can be direct or indirect by modifying environmental conditions or competitive interactions, to maintain their vigour (Fynn et al. 2005a). Fire is an important disturbance, it increases tiller production of perennial palatable grasses that are important for livestock production (Uys et al. 2004). Most of the palatable grass species are sensitive to shading and fire removes the dead moribund material which would otherwise shade these species (Fynn et al. 2011). Fire has been shown to be interchangeable with mowing in maintaining the vigour of the desired palatable grass species, since mowing similarly to fire is a uniform non-selective disturbance (Fynn et al. 2004).

Grazing is a selective disturbance and grazing herbivores differentially select certain areas which end up being overgrazed over others which would be leniently grazed (Hatch and Tainton 1990). The selected preferred patches would usually consists of palatable perennial grass species such as *Themeda triandra* (Tainton et al. 1999). Although the perennial palatable grass species can withstand some grazing, under higher stocking rates, the degree of selectivity on the preferred palatable species increases, leading to severe and frequent defoliation which reduces tiller numbers and size of the preferred palatable species (Morris and Tainton 1993). Heavy grazing on palatable grass species reduces their competitive abilities when competing for resources with ungrazed unpalatable grass species (Fynn et al. 2005b). Grazing herbivores can also modify the microclimate around the grazed patches by increasing the soil nutrient content from dung and urine which can be used by the grazed plants for regrowth (Schuman et al. 1999). However the addition of soil nutrients in the nutrient limited mesic grasslands have been shown to reduce the abundance of palatable grasses on mesic grasslands (Fynn and O'Connor 2005). Hence, the excessive nutrient accumulation which may occur with high stocking rates and densities under HDG might be detrimental to the palatable grasses.

Conventional rotational grazing systems use fire and grazing interactively (Kirkman and Moore 1995), with the grazing recommended at lenient stocking rates to maintain mesic grasses in good condition (Little et al. 2015). Fire in the absence of grazing has been shown to maintain high grass species richness (Kirkman et al. 2014). There is no empirical data showing that grazing in the absence of fire on mesic grasslands can maintain high grass species richness and the vigour of the desired palatable grasses as contended for the HDG system. Grazing animals are selective and under high stocking rates and density which are advocated for under HDG systems that may put more pressure on the palatable species. As a consequence, the palatable species may decline in abundance or get replaced by the unpalatable species (Tainton 1972). Additionally, excessive moribund or dead material would be expected to build up in the absence of fire and shade out the shade sensitive palatable species (Everson et al. 1988).

2.4.3.2 Forbs

Forb species contribute most to plant diversity in grasslands and are also economically important for livestock production (Bullock et al. 2001, Spehn et al. 2002, Morris 2004, Provenza et al. 2009). The legume perennial forb species are a natural source of nitrogen for livestock (Ehui et al. 1998). Legumes generally have high levels of nitrogen and their digestibility declines less rapidly compared to perennial mesic grasses (Carlsson and Huss-

Danell 2003). Hence they play a critical role in supplying nitrogen to livestock when grazed late in the growing season or in the non-growing season when the quality of the grasses is low (Van der Hoek 1998). Some legume species can fix nitrogen and benefit their neighbouring grasses and non-legume forbs by transferring nitrogen to them (Temperton et al. 2007). The presence of legumes have also been shown to increase species richness in degraded grasslands (Hu et al. 2016). Other forb species are selected for by livestock not because they directly contribute towards forage quality but because they contribute chemically to the digestive process (Provenza et al. 2009), while other forbs have medicinal properties for livestock for example inhibit intestinal parasites (Forbey et al. 2009, Lisonbee et al. 2009). Given the biodiversity and economic value of forbs it is important to understand how the key disturbances, fire and grazing, affect forb species composition.

Mesic forbs are mostly long-lived perennials that regenerate annually in spring from underground storage organs such as rhizomes, tubers, corms and bulbs (Bews 1925, Carbutt et al. 2011). Fire stimulates resprouting of the mesic forbs from their underground storage organs and opens up the habitat for the forbs to emerge by removing the grass overstorey (Bews 1925, Bond and Parr 2010). The exclusion of fire on South African grasslands for more than 10 years resulted in a decline in forb species richness and species shifts, perennial long-lived forb species were replaced by the ruderal weedy perennials and annual species (Fynn et al. 2004, Uys et al. 2004). This indicates that fire is an important disturbance for the persistence of South African mesic forbs (Uys 2006a). On the contrary, the exclusion of fire on similar grasslands in North America increases forb species richness (Smith et al. 2016). An intercontinental study conducted on North American and South African mesic grasslands found that more frequent fires decreased forb species richness in North America while in South African mesic grasslands forb species richness increased (Kirkman et al. 2014). Differences in the response of forbs in the two continents could be due to the evolutionary history of forbs (Smith et al. 2016). Most South African mesic forbs possess underground storage organs from which they resprout after fires (Zaloumis 2013) while North American forbs have not been shown to have underground storage organs and that may render them weaker competitors against the grasses (Elson and Hartnett 2017). North American forbs are more susceptible to competition from the grasses and studies have shown that more frequent fires favours grasses over forbs (Smith et al. 2016). Findings from the intercontinental studies highlighted the need for studying and understanding that each system can be unique and generalizing findings from one system to others do not always work.

Grazing affects forb species either directly through consumption and trampling or indirectly by modifying competitive interactions and resource availability (Archer and Smeins 1991, Huntly 1991). Although the consumption of forbs does not contribute significantly to forage intake compared to grasses, grazing animals often select forbs at higher rate than their contribution to the biomass (Fahnestock and Knapp 1994, Hartnett et al. 1996). The selection of forbs is based on a number of factors including their palatability and growth habit (Cid and Brizuela 1998). Palatable erect forbs are more susceptible to being grazed because they are more visible compared to prostrate palatable growth habits (Hickman and Hartnett 2002). Trampling of forbs unlike consumption is more random and forb species that are likely affected include those with broad leaves, fleshy stems and leaves as well as trailing plant parts (O'Connor 2005).

South African mesic grassland studies that have shown that high grazing pressure or higher stocking rates results in a loss of plant diversity and a shift from long-lived to more ruderal-like forb species (Uys 2006b, O’Connor et al. 2011, Scott-Shaw and Morris 2015). In contrast to the above findings, in the American prairie, high grazing pressure resulted in an increase of forb diversity, however this increase was mainly due to an increase of indigenous annual forb species (Hickman et al. 2004). Annual forbs have been shown to be favoured by high grazing pressure over perennial forbs (O'Connor 1991a, Diaz et al. 2007). Hence, a species shift from long-lived forb species to the short lived ones may have occurred in the American prairie. Annuals are not usually of conservation concern but rather many long-lived perennials, particularly in the South African mesic grasslands are important. The impact of various grazing systems on forb diversity in the South African mesic grasslands is not known but with the high stocking rate and stocking density coupled with the absent of fire under HDG compared to conventional grazing systems, a species shift is expected.

2.4.3.3 Functional traits

Functional traits are defined as the morphological, physiological, structural or life history attributes of plants that characterises a response to a disturbance (Pausas et al. 2004, Klimesova et al. 2008). Diversity indices may not be appropriate for assessing plant diversity responses due to the potential species turnover under the various grazing systems (O'Connor et al. 2010). Hence to understand the impact of grazing systems on plant diversity, appropriate functional traits need to be identified, particularly for the forbs, since grasses have received considerable attention (Wolfson and Tainton 1999). The use of species’ functional traits rather than species names, also helps to compare responses between sites that do not share species (O'Connor et al. 2010). Functional traits that have shown a consistent response to grazing include life history (annuals vs perennials) and growth habits (prostrate vs erect), with high grazing pressure favouring annuals over perennials and prostrate over erect plants (Uys 2006b, Diaz et al. 2007). However, how these functional traits respond under the various grazing systems is not known.

2.4.4 Forb demography

The composition and structure of grasslands is known to be shaped by different factors, grazing being one of them (O'Connor 1994). To better understand compositional changes due to grazing, the population mechanisms of the dominant species need to be determined (O’Connor 1994). Demography and life history attributes are some of the population mechanisms that can influence the extinction or persistence of species (Williams 1970, O'Connor 1991b). The effect of grazing on the population mechanisms of grasses has been determined for the South African grasses (O'Connor 1993, 1994, O’Connor and Everson 1998) but not so much for the forbs (Uys 2006b). To maintain a healthy stable grassland it is crucial to understand the impact of heavy grazing under HDG on the population mechanisms that drive compositional changes of forbs, particularly in the mesic grassland where reproduction is mainly vegetative and seed recruitment plays a minor role (Everson 1994, Uys 2006b).

2.4.5 Forb responses to grazing and interspecific competition

Grazing modifies the competitive interactions between plants within grassland communities by favouring certain species and reducing the competitive ability of others (Vesk and Westoby 2002). Selective herbivory reduces the competitive ability of the palatable grasses because they are selected for and that leads to their replacement by unpalatable grasses which are usually avoided and have a competitive advantage (Vesk and Westoby 2002). This grazing induced shift led to the development of the increaser-decreaser concept, which is well applied to the South African grasses but not so much for the forbs (Foran et al. 1978).

Plants growing in close proximity are likely to compete for the same resources such as light, soil nutrients and water (Jensen and Löf 2017). Grasses are known to be strong competitors when competing with trees (Bond 2008, Cramer et al. 2010). However, the competitive interactions between grasses and forbs are less studied in the South African mesic grasslands (Zaloumis 2013).

In South African mesic grasslands, forbs alter their growth habits in response to grass competition (Zaloumis 2013). The erect forb species adjusted their height by growing taller while prostrate ones with wide leaves made their leaves wider, in the presence of grass competition for light (Zaloumis 2013). In the above study, however both the grasses and forbs were not defoliated.

Plant community interactions are not always competitive but can also be facilitative (Schoener 1982, Brooker et al. 2007). Facilitation is the positive or beneficial interaction between plants (Hunter and Aarssen 1988). For decades research considered facilitation interaction to only occur in successional communities (Clements 1916, Chapin et al. 1994), whereby a plant community modifies the environment and make it easy for the next type of plant community to occupy that area. This view was later challenged; in the late 1980s a number of studies showed that facilitative interactions not only operated during successional stages but also through direct and indirect positive interactions between species in stable non-successional communities (Hunter and Aarssen 1988, Bertness and Callaway 1994, Callaway 1997, Brooker and Callaghan 1998). An example of facilitation in mesic grasslands, is a legume forb that fixes nitrogen and transfer it to the neighbouring grasses (Temperton et al. 2007). However, very few studies have assessed the interaction between grasses and forbs, in the presence of other disturbances such as grazing (Del-Val and Crawley 2004). It is important to gain an understanding of this interaction under HDG system because forbs are likely to be defoliated either by grazing or trampling due to the high stocking rate and density.

2.5 Conclusions

The importance of conserving high plant diversity in South African mesic grasslands for ecosystem and economic value has been realised. The majority of the natural mesic grasslands are under livestock production hence in order to conserve plant diversity understanding the effects of different grazing systems is important. Forbs constitute most of the plant diversity in grasslands yet factors that determine their abundance and species richness are less known compared to the grasses which constitutes most of the biomass. Understanding the effects of HDG, which is an extreme rotational grazing system on mesic grasslands is of particular importance. HDG advocates the replacement of fire with high density grazing under higher stocking rates compared to conventional rotational grazing systems. Mesic grasslands are a fire dependent system and the exclusion of fire results in species composition shifts with the fire dependent species being replaced by the fire independent species (Uys et al. 2004, Kirkman et al. 2014). High stocking rates or heavy grazing reduces plant diversity in mesic grasslands (Uys 2006b, Scott-Shaw and Morris 2015). However, a lot of the studies on South African mesic grasslands have looked at fire alone or the interaction between fire and grazing but the effect of replacing fire with high density grazing at higher stocking rates as under the HDG system is yet to be determined.

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CHAPTER 3: WHAT ARE THE LONG-TERM EFFECTS OF HIGH-DENSITY, SHORT-DURATION STOCKING ON THE SOILS AND VEGETATION OF MESIC GRASSLAND IN SOUTH AFRICA?

3.1 Abstract

High density, short duration stocking (HDG) is gaining popularity amongst farmers in the South African mesic grasslands, but little is known about its potential impact on natural resources. Using a fence-line contrast approach, this study compared the long-term effects of HDG with those of other rotational grazing systems at lower densities (LDG) on soil properties and vegetation composition at two sites. Soils from Kokstad and Cedarville were 31% and 19% more compacted under HDG than LDG, respectively, but did not differ in total nitrogen, total carbon, available phosphorus or pH. At Kokstad, HDG had promoted unpalatable grass species at the expense of palatable grass species. Forb species composition differed substantially between HDG and LDG, with HDG having 13 and LDG having16 unique species. A radical prostrate growth habit was favoured over a cauline erect habit under HDG. At Cedarville, few grass or forb species showed differences between HDG and LDG, possibly because of an overriding influence of the absence of burning in both grazing systems. These results suggest that HDG potentially has negative impacts on soil health and vegetation composition of South African mesic grassland.

Keywords: *biodiversity, grazing management systems, forbs*

3.2 Introduction

Holistic Management™ advocates time-controlled rotational stocking of livestock at high density in paddocks for short durations (HDG), which is a flexible, goal-directed strategy aimed at maintaining or restoring vegetation cover, soil health, biodiversity and achieving high livestock production (Savory 1983, Savory and Butterfield 2016). Under HDG, multi-paddocks or herding are used to concentrate large herds on small areas of land for a short duration to achieve even use of available forage, followed by adequate rest periods to allow perennial grasses and forbs (herbaceous dicotyledons and non-graminoid monocotyledons) to recover (Savory and Parsons 1980). HDG is postulated to improve soil health by breaking the soil crust through hoof action to alleviate compaction, and by increasing nutrient availability through an increased rate of nutrient cycling from standing dead herbage to soils and from high concentrations of dung and urine in paddocks (Savory and Butterfield 2016).

High-density, short-duration stocking is currently gaining popularity amongst farmers in South African mesic grasslands (Zietsman 2010, Phillips 2014) owing to the claimed benefits, which are said to result in greater profits compared with other grazing systems (Savory and Butterfield 2016). Concentrated large herds of livestock, rather than fire, are advocated as a tool to remove standing dead herbage at the end of the dry period and to allow litter to accumulate for the purpose of protecting soil moisture (Savory and Butterfield 2016). Grazing management systems commonly used by commercial farmers in South African mesic grasslands include variations of the flexible stocking rotational grazing with at least one paddock rested for a full season on a rotational basis and they include burning (Venter and Drewes 1969, Kirkman and Moore 1995). These conventional rotational stocking systems apply moderate stocking rates and stocking densities much lower than those advocated for HDG (O’Connor et al. 2010). South African mesic grasslands evolved with fire and grazing animals and are thus adapted to these disturbances (Stuart-Hill and Mentis 1982, Tainton and Mentis 1984). However, it is moderate grazing and burning that sustains high plant diversity on these grasslands (Uys et al. 2004, Joubert et al. 2017) and on similar grasslands globally (Hart and Ashby 1998; Dumont and Tallowin 2011). Grasses are well adapted to grazing and trampling (Briske and Richards 1995) but many forbs, which comprise the bulk of species diversity in grasslands (Uys 2006), are likely less resistant to herbivory than grasses (O’Connor et al. 2010, Scott-Shaw and Morris 2015, Chamane et al. 2017).

Fire plays an important role in grassland functioning globally (Briggs and Knapp 1995, Lunt and Morgan 2002) and in South Africa (Snyman and Cowling 2004, Briggs et al. 2005, Palmer and Ainslie 2005). In mesic grasslands, frequent fires increase tiller production of most palatable grasses such as *Themeda triandra*, with seedling recruitment playing only a minor role in their regeneration (Everson et al. 1985, Trollope 1999, Everson et al. 2009). Fire also stimulates resprouting of most mesic grassland forb species from their underground storage organs (Fynn et al. 2004). Excluding fire can result in a shift in forb species composition (Titshall et al. 2000, Fynn et al. 2005), with fire-tolerant species being replaced by fire-intolerant species.

A fence-line between two properties managed differently may divide areas with similar soil and climate, thereby allowing assessment of the effects of grazing management with other factors equal (Noy-Meir et al. 1989). Fence-line studies are especially useful when the management histories are well known and the ‘treatments’ have been consistently applied on opposite sides of the fence for at least a decade (Teague et al. 2008, Zimmermann 2009). The aim of this study was to use a fence-line contrast between neighbouring commercial farmers to determine the long-term (15+ years) impact of HDG compared to low density stocking in a conventional rotational grazing system (LDG) on soil physical and chemical properties and vegetation structure and composition of South African mesic grassland. The following specific questions were addressed. i.) Will the physical (compaction) and chemical (pH, available phosphorus, total nitrogen and total carbon) properties of the soil be improved under HDG compared to LDG? ii.) Under HDG, is vegetation cover and litter mass improved? iii.) Will species composition and diversity of grasses and forbs be improved under HDG compared to LDG?

3.3 Materials and methods

3.3.1 Climate, soil and vegetation

The two study areas were located outside Kokstad (30.47888° S, 29.51795° E) in KwaZulu-Natal and Cedarville (30.45637° S, 29.03597° E) in the Eastern Cape Province, South Africa. The study sites at Kokstad and Cedarville were selected because that is where the high density, short duration grazing farms in the mesic grasslands had been running for a long-term (> 10 years) and the farmers were willing to collaborate. Both sites were at an elevation of approximately 1 500 m a.s.l., and receive about 780 mm annual precipitation (coefficient of variation of 20%), occurring mainly during the summer growing season (October – April) (Dent et al. 1987). Summers are warm to hot with a mean daily maximum of 25ºC in January. Winters are cool with regular frost and a mean daily minimum temperature of 2.1ºC in July. The geology of the region consists of mudstone and sandstone of mainly the Beaufort group of the Karoo sequence (Mucina et al. 2006). The soils are of Hutton and Clovelly forms on sediments and Shortlands on dolerite and mainly have a clay-loam texture (Soil Classification Working Group 1991). Vegetation is classified as East Griqualand Grassland (Gs 12) consisting of mainly grassland with patches of bush clumps dominated by *Leucosidea sericea* (Mucina et al. 2006).

3.3.2 Study approach

At each site, a fence-line contrast study was conducted between two properties. One had been stocked with cattle in a short duration rotational system at a high density (HDG) and the other was a rotational grazing system at a much lower density (LDG). With this fence-line design, we acknowledge that our sampling plots are pseudo replicated (Hurlbert 1984). However, we feel that the common difficulty in obtaining treatment replicates in long-term or natural experiments is widely acknowledged to be offset by the rich information gained from these systems (Davies and Gray 2015). We also acknowledge that our replicates are not independent treatment replicates. However, considering the plots are directly adjacent either side of the fence with similar biotic and abiotic characteristics, we consider it reasonable to interpret changes due to management (including grazing, fire, animal density and stocking rate).

At Kokstad, the two properties were owned by different producers, with Braford and Bonsmara cattle breeds run on the HDG and LDG systems, respectively. HDG had been running for >17 years and LDG for 30 years by 2015, when it was sampled. The HDG property at Kokstad had not been burned for 19 years whereas the LDG property had been burned every 2 – 4 years in early spring. HDG had double the number of animal units (AU), greater than ten-fold stocking density, rapid rotation in smaller paddocks and similar recovery / rest period compared to LDG (Table 3.1). The previous grazing system on both properties was low density continuous grazing of cattle and sheep.

At Cedarville, both properties were owned by one farmer who managed the HDG operation using a mixed breed and leased out the LDG side on which Bonsmara cattle were run. HDG and LDG had been running for 15 years by 2016, when they were sampled. Although the owner discourages burning for both systems, a runway fire in 2006 burned both properties making it 10 years since the last burn in 2016. HDG had double the animal units (AU), four-fold stocking density, rapid rotation on half the size of LDG paddocks and a recovery / rest period 40 days shorter under HDG than LDG (Table 3.1). The previous grazing system on both properties was a four camp rotational stocking system with a rotational burn one quarter of the farm every year.

Table 3.1: Details of grazing management for high-density, short-duration stocking (HDG) and rotational grazing system at low density (LDG) systems at Kokstad and Cedarville

Management variable	Kokstad		Cedarville	
Grazing system name	HDG	LDG	HDG	LDG
Total size of grazing area (ha)	250	280	540	530
Mean herd size (AU)*	218	100	400	225
Number of paddocks	16	4	15	5
Mean paddock size (ha)	15	70	50	100
Mean period of occupation (days)	7	40	7	160
Mean period of absence (days)	120	120	70	120

Stocking density (AU ha^{-1})	15	1	8	2
Total frequency grazed per annum	2-3	2-3	2-3	2

*One AU is defined as equivalent to one cow, weighing 450 kg which gains 0.5 kg per day on forage with a digestible energy percentage of 55% (Trollope et al. 1990)

3.3.3 Soil physical and chemical properties

At each site, a total of 20 paired 10 x 10 m plots were located along the fence down a slope at 10 m intervals between HDG and LDG systems to measure soil physical and chemical properties, litter mass, litter depth, plant species composition, and forb growth habits. Each pair of plots was located at 15 - 30 m from the fence to the edge of the plot in order to avoid possible confounding effects of fire breaks and livestock trampling close to the fence. Each pair was matched as closely as possible for slope, aspect, rock cover and soil type.

Soil compaction was measured as resistance to penetration (J m^{-1}) using a dynamic cone penetrometer (Herrick and Jones 2002). Three measurements were taken per plot, one in the centre and one 2 m on either side. For each reading, a weight of 2 kg was dropped 40 cm for five strikes, and the depth the penetrometer shaft entered the soil was recorded for each strike.

Soil samples were collected from the surface down to 10 cm depth using a soil auger. Three samples were collected in every second pair of plots and the three subsamples from the same plot were combined to provide a composite sample. There were thus 10 paired composite samples along a fence line. Soil samples were air dried and then analysed using a CNS analyser at the Cedara soil science laboratory of the KwaZulu-Natal Agriculture and Environmental Affairs for soil pH and available phosphorus using the Hunter method, and total carbon and total nitrogen by Dumas combustion (Barnard et al. 1990).

3.3.4 Litter mass and litter depth

Litter, defined as dead detached plant material on the soil surface, was measured inside each plot using five randomly placed 0.25 m^2 quadrats. Litter depth was sampled by pushing a 3 mm diameter pin through the litter to the soil surface inside the quadrat and measuring the highest horizontal dead-plant material (Hayes and Holl 2003). All the litter in the five quadrats was collected, oven dried at 60ºC for 72 hours and then weighed.

3.3.5 Plant species composition and forb growth habits

In each 10 x 10 m plot, a 0.25 m^2 quadrat was randomly placed 20 times to determine plant species composition, species abundance, and forb growth habits. In each quadrat, grass and forb species were identified and recorded. The percent cover of each grass species rooted in the quadrat was visually estimated to the nearest 5% (Burns et al. 2009) and species composition was expressed as the mean cover percent of each species per plot. The abundance of each forb species was quantified by counting the number of individuals per species rooted in each quadrat, expressed as mean density per plot. Nomenclature followed POSA (SANBI: Plants of Southern Africa – an online checklist; http://www.posa.sanbi.org). Above-ground growth habits of forb species were identified according to their presumed competitiveness in a grass sward for light, grouped according to the following categories: cauline erect, cauline prostrate, radical erect, and radical prostrate. This classification was based on the point of leaf emergence (cauline = from stem and radical = at or below ground) and plant orientation (erect or prostrate) (Uys 2006; Diaz et al. 2007). The proportion of forbs with each growth habit was calculated from the forb density data.

3.3.6 Ground cover

Six paired 50 m transects were laid out at right angles to and either side of the fence to minimize spatial variability, to measure ground cover using a modified point intercept method (Naeth et al. 1991). There was 15 - 30 m distance from the fence to the edge of a transect to control for edge effect and fire breaks on both sides of the fence. The paired transects were located at 10 m intervals. A sampling pole with 3 mm diameter pin was dropped 100 times, every 0.5 m, along each transect and strikes of the following ground cover categories were recorded: live vegetation (when the pin touched the base of a plant), bare soil, rock or litter.

3.3.7 Statistical analysis

Management had been different at Kokstad and Cedarville. Hence, the analysis for each site were separate. The chosen level of significance for all statistical analysis was $p \leq 0.05$.

A paired t-test was used to determine whether soil physical and chemical properties (soil compaction; soil total C (%), total N (%), available phosphorus and pH); ground cover categories (live vegetation, bare soil, rock and litter); litter depth; litter mass and plant species diversity differed between HDG and LDG. Diversity was expressed as (1) Shannon-Weiner diversity index (H′), (2) Pielou’s evenness (J′) and (3) species richness (Magurran 2004). The Shannon-Weiner diversity index and evenness were calculated using the forb abundance and grass percentage cover data separately per 1 m^2 per plot. Species richness was the mean number of grass and forb species separately per m^2, assessed from a total area of 5 m^2 from 20 quadrats per plot. Grasses and forbs were analysed separately to determine their potentially different response (Fynn et al. 2004).

Partial redundancy analysis (pRDA), a direct gradient multivariate analysis technique was used to examine whether the different grazing systems (HDG and LDG) accounted for the pattern of grass and forb compositional variation as well the variation in forb growth habits, using the CANOCO 4.5 package (Ter Braak 2009). Partial ordination was used to account for spatial differences along the fence-line by specifying the paired plot location as a dummy covariable. An initial detrended correspondence analysis indicated the species turnover of grasses and forbs were both sufficiently low to employ RDA, which assumes a linear response model. Grazing system effects (HDG vs LDG) independent to spatial variability were fitted and tested with a Monte Carlo permutation test (999 permutations) restricted within locations. Species that only appeared once were excluded from the analysis.

3.4 Results

3.4.1 Soil properties and vegetation structure

Soils from Kokstad and Cedarville were 31% and 19% more compacted under HDG than LDG, respectively, but grazing treatments did not otherwise differ for any chemical property at either study site (Table 3.2). Litter mass was higher under HDG at both study sites, up to twice as much for Cedarville (Table 3.3). At Kokstad, the ground cover variables did not differ between HDG and LDG (Table 3.3). However, at Cedarville, where fire had been excluded for 10 years under both HDG and LDG, litter cover was higher and live vegetation cover was 17 % less under HDG than under LDG (Table 3.3).

Table 3.2: Soil physical (compaction measured as resistance to penetration) (n = 20) and chemical properties (n = 10) (mean ± SE) under high-density, short-duration stocking (HDG) and low-density stocking (LDG) systems at Kokstad and Cedarville, South Africa, assessed using a paired t-test. Values in bold are significant at $p \leq 0.05$

Variable	HDG	LDG	t	df	p
Kokstad					
Soil compaction ($J\ m^{-1}$)	686.00 ± 32.667	473.70 ± 62.594	3.03	19	**0.014**
Soil N (%)	0.31 ± 0.042	0.31 ± 0.029	0.39	9	0.708
Soil C (%)	4.45 ± 0.478	4.43 ± 0.264	0.13	9	0.902
P ($mg\ L^{-1}$)	5.90 ± 1.972	5.40 ± 1.020	0.71	9	0.495
Soil pH (KCl)	4.70 ± 0.184	4.60 ± 0.123	0.16	9	0.879
Cedarville					
Soil compaction ($J\ m^{-1}$)	369.18 ± 19.844	300.10 ± 21.454	2.10	19	**0.049**
Soil N (%)	0.21 ± 0.006	0.21 ± 0.007	0.34	9	0.742
Soil C (%)	2.87 ± 0.736	2.90 ± 0.639	0.43	9	0.680
P ($mg\ L^{-1}$)	6.40 ± 0.476	6.10 ± 0.504	0.56	9	0.591
Soil pH (KCl)	5.09 ± 0.045	5.00 ± 0.054	1.61	9	0.142

Table 3.3: Litter and ground cover variables (mean ± SE) of mesic grassland under high-density, short-duration stocking (HDG) and low-density stocking (LDG) examined using a paired t-test (values in bold are significant at $p \leq 0.05$) at Kokstad and Cedarville, South Africa, assessed using a paired t-test.

Variables	HDG	LDG	t	df	p
Kokstad					
Litter mass (g m^{-2})	321.0 ± 14.53	186.2 ± 9.63	7.193	19	**<0.0001**
Litter depth (cm)	2.7 ± 0.19	2.5 ± 0.15	0.597	19	0.557
Litter cover (%)	40.2 ± 3.06	32.3 ± 1.45	2.482	5	0.056
Live vegetation (%)	57.0 ± 2.50	55.8 ± 1.83	0.483	5	0.649
Bare ground (%)	2.8 ± 1.01	0.8 ± 0.40	2.148	5	0.084
Cedarville					
Litter mass (g m^{-2})	79.6 ± 11.57	34.0 ± 3.94	4.295	19	**< 0.0001**
Litter depth (cm)	1.6 ± 0.13	1.3 ± 0.09	1.954	19	0.066
Litter cover (%)	31.2 ± 1.78	14.5 ± 6.02	2.972	5	**0.031**
Live vegetation (%)	63.3 ± 1.38	76.2 ± 4.14	2.506	5	**0.054**
Bare ground (%)	5.5 ± 2.51	9.3 ± 3.16	1.635	5	0.163

3.4.2 Plant species composition and diversity

3.4.2.1 Kokstad

HDG and LDG shared 25 grass species, grass species richness was similar between the grazing systems, but Shannon-Weiner diversity and evenness were higher under HDG compared to LDG (Table 3.4). The diversity indices (Table 3.4) did not differ for the forb species composition between HDG and LDG. However, Jaccard's dissimilarity index, indicated a forb species turnover of 32%, with HDG having 13 and LDG 16 unique species.

A pRDA with the Monte Carlo permutation indicated that grazing system accounted for grass (pseudo-F = 8.0, p = 0.0001) and forbs (pseudo-F = 5.2, p = 0.0001) species variation. The first axis of the pRDA, representing the variation in species composition attributable to grazing after accounting for spatial variability, accounted for 29.7% for grasses (Figure 3.1a, Table 3.5) and 21.4% for forbs (Figure 3.2a, Table 3.6). The species whose variance was well accounted for by the pRDA (> 10%) were mainly those which exhibited a significant response in a paired t-test between HDG and LDG (Table 3.7). Of the 21 grass species tested, most of the unpalatable species (*Alloteropsis semialata*, *Brachiaria serrata*, *Eragrostis curvula*, *Eragrostis plana* and *Microchloa caffra*) had a higher percentage cover under HDG while the palatable species (*Hyparrhenia hirta*, *Themeda triandra* and *Trachypogon spicatus*) had a lower percentage cover compared to LDG (Figure 3.1a, Table 3.7). For the 61 forb species tested, only three forbs including an alien ruderal species (*Eriosema cordatum, Senecio speciosa* and *Taraxacum officinale*) were more abundant under HDG compared to LDG where nine forb species were more abundant (*Acalypha schinzii*, *Eriosema distinctum*, *Eriospermum abyssinicum*, *Helichrysum aureonitens*, *Helichrysum herbaceum*, *Pachycarpus sp*, *Pentanisia prunelloides*, *Senecio bupleuroides* and *Stachys natalensis*) (Figure 3.2a, Table 3.7). Forbs with a radical prostrate growth habit were more common over cauline erect forbs under HDG (pseudo-F = 5.3, p = 0.0081) (Figure 3.3).

3.4.2.1 Cedarville

There was a grass species turnover of 23% as reflected by the Jaccard dissimilarity index, with HDG having four unique species while LDG had one. HDG had a low Shannon-Weiner diversity and evenness of grass species compared with LDG, although grass species richness was similar between HDG and LDG (Table 3.4). Shannon-Weiner diversity and species richness of the forb species was not affected by grazing system but the forb evenness was slightly higher under HDG compared to LDG (Table 3.4). HDG and LDG had similar species and there was a small species turnover (21%) as reflected by the Jaccard dissimilarity index, with HDG having six unique species while LDG had five.

A pRDA with the Monte Carlo permutation revealed that HDG and LDG accounted for grass and forb species variation, with axis one accounting for 26.4% for grass (pseudo-F = 6.8, p = 0.0010) (Figure 3.1b, Table 3.5) and 16.7% for forb species (pseudo-F = 3.4, p = 0.0040) (Figure 3.2b, Table 3.6) variance. Of the 16 grass species tested, only one palatable species (*Themeda triandra*) had a higher percentage cover under HDG and one unpalatable species (*Eragrostis capensis*) had a higher percentage cover under LDG (Figure 3.1a, Table 3.7). For the 36 forb species tested, three forb species (*Commelina africana*, *Helichrysum aureonitens* and *Rhynchosia cooperi*) were more abundant under HDG, compared to LDG, where only one forb species was more abundant (*Hermannia depressa*) (Figure 3.2b, Table 3.7). The impact of HDG on forb above-ground growth habit was marginally non-significant (pseudo-F = 2.283, p = 0.0730) because only a few forb species were affected by grazing system.

Table 3.4: Mean (±SE) evenness (J′), Shannon-Weiner diversity (H′) of forb species at Kokstad and Cedarville at high-density, short-duration stocking (HDG) and low-density grazing (LDG) assessed using a paired t-test. Values in bold are significant at $p \leq 0.05$

Variables	HDG	LDG	t	df	p
Kokstad					
Grass J′ (m^{-2})	0.52 ± 0.015	0.47 ± 0.015	2.520	19	**0.021**
Grass H′ (m^{-2})	1.67 ± 0.048	1.51 ± 0.047	2.954	19	**0.008**
Grass richness (m^{-2})	1.21 ± 0.053	1.25 ± 0.054	0.515	19	0.612
Forb J′ (m^{-2})	0.60 ± 0.008	0.58 ± 0.013	1.029	19	0.316
Forb H′ (m^{-2})	2.59 ± 0.034	2.52 ± 0.055	1.029	19	0.316
Forb richness (m^{-2})	5.19 ± 0.183	5.24 ± 0.220	-0.252	19	0.804
Cedarville					
Grass J′ (m^{-2})	0.53 ± 0.018	0.61 ± 0.017	3.290	19	**0.004**
Grass H′ (m^{-2})	1.55 ± 0.054	1.72 ± 0.049	2.372	19	**0.028**
Grass richness (m^{-2})	1.63 ± 0.772	1.77 ± 0.548	1.437	19	0.167
Forb J′ (m^{-2})	0.57 ± 0.015	0.49 ± 0.040	2.088	19	**0.050**
Forb H′ (m^{-2})	2.18 ± 0.058	1.86 ± 0.152	2.008	19	0.059
Forb richness (m^{-2})	3.11 ± 0.135	2.88 ± 0.126	1.363	19	0.189

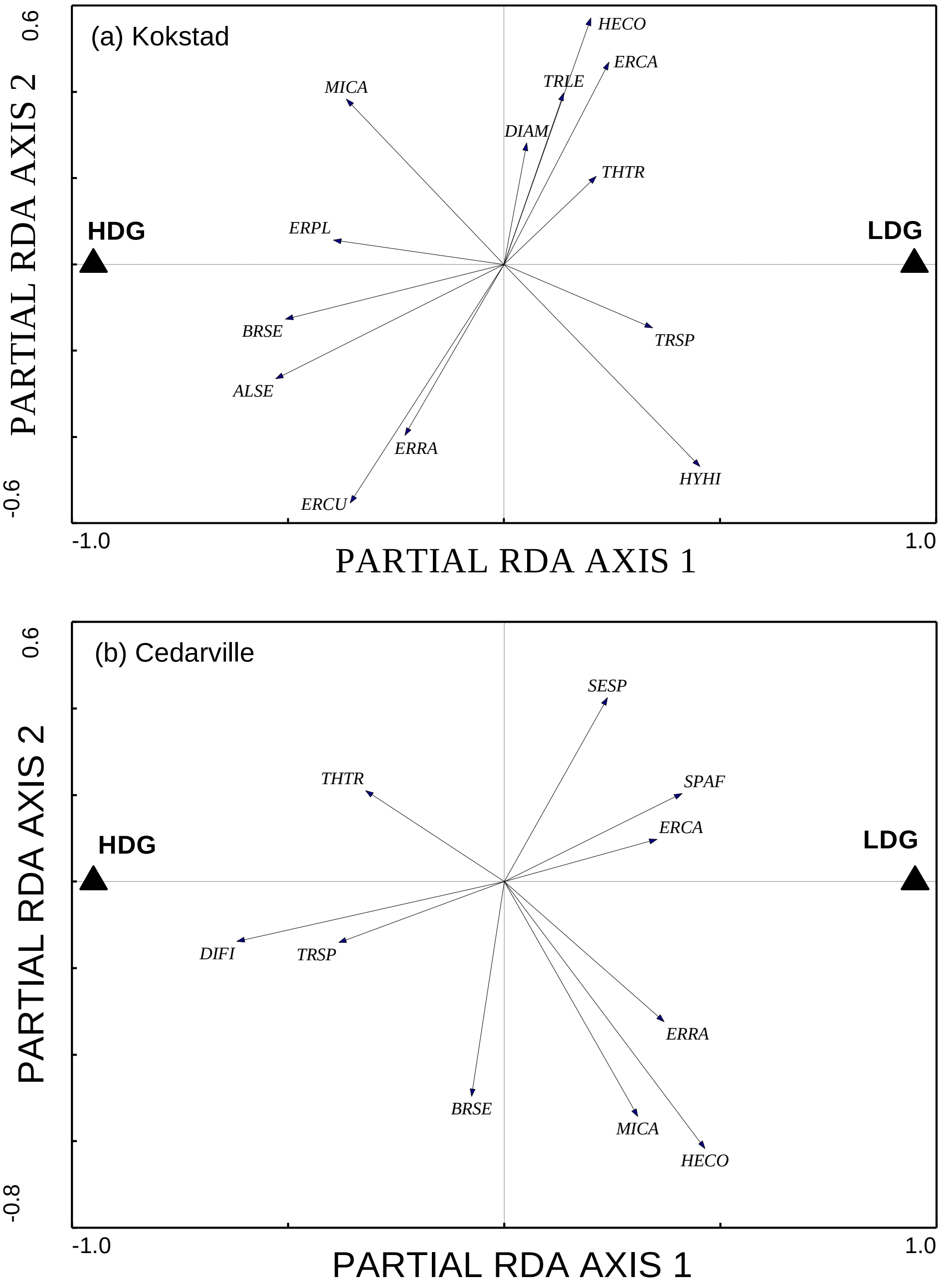

Figure 3.1: Plot of species on the first two axes of a partial redundancy analysis (pRDA) of grass species composition data from a fence line study between high density, short duration stocking (HDG) and low density stocking (LDG) systems at (a) Kokstad and (b) Cedarville, n = 40 for each site. Only species with at least 10% of their variation explained are shown. Key to species: ALSE = *Alloteropsis semialata*, BRSE = *Brachiaria serrata*, DIAM = *Diheteropogon amplectens*, DIFI = *Diheteropogon filifolius*, ERCA = *Eragrostis capensis*, ERCU = *Eragrostis curvula*, ERPL = *Eragrostis plana*, ERRA = *Eragrostis racemosa*, HECO = *Heteropogon contortus*, HYHI= *Hyparrhenia hirta*, MICA = *Microchloa caffra*, SESP = *Setaria sphacelata*, SPAF = *Sporobolus africanus*, THTR= *Themeda triandra*, TRSP= *Trachypogon spicatus* and TRLE = *Tristachya leucothrix*

Table 3.5: Summary of a partial redundancy analysis (pRDA) of the effect of grazing system (HDG vs LDG) on grass species composition (n = 40), after controlling for spatial variability, at Kokstad and Cedarville

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Kokstad				
Eigenvalue	0.112	0.104	0.043	0.023
Cumulative variation explained (%)[1]	29.72	57.37	68.68	74.75
Pseudo-canonical correlation	0.910			
Cedarville				
Eigenvalue	0.120	0.132	0.048	0.038
Cumulative variation explained (%)[1]	26.40	55.60	66.10	74.50
Pseudo-canonical correlation	0.874			

[1] Percentage of the residual variance accounted for after fitting covariables.

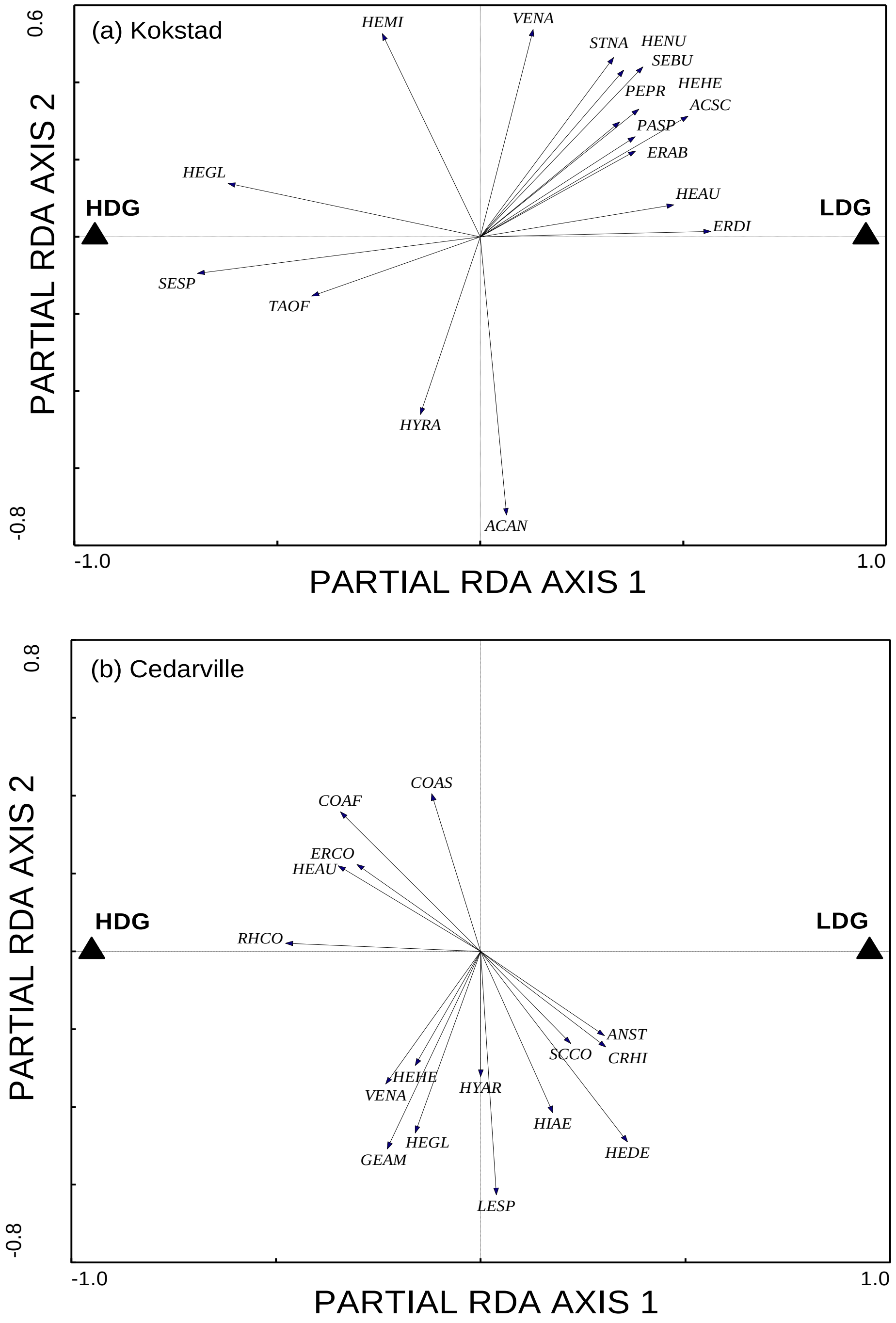

Figure 3.2: Plot of species on the first two axes of a partial redundancy analysis (pRDA) of forb species composition data from a fence line study between high density, short duration stocking (HDG) and low density stocking (LDG) systems at (a) Kokstad and (b) Cedarville, n = 40 for each site. Only species with at least 10% of their variation explained are shown. Key to species: ACAN = *Acalypha angustata*, ACSC = *Acalypha schinzii*, ANST = *Anthospermum streyi*, COAF = *Commelina africana*, COAS = *Corchorus asplenifolius*, CRHI = *Crabbea hirsuta*, ERCO = *Eriosema cordatum*, ERDI = *Eriosema distinctum*, ERAB = *Eriospermum abyssinicum*, GEAM = *Gerbera ambigua*, HEAU = *Helichrysum aureonitens*, HEDE =

Hermannia depressa, HEGL= *Helichrysum glomeratum*, HEHE = *Helichrysum herbaceum*, HEMI = *Helichrysum miconiifolium*, HENU = *Helichrysum nudifolium*, HIAE = *Hibiscus aethiopicus*, HYAR = *Hypoxis argentea*, LESP = *Ledebouria* sp, PASP = *Pachycarpus* sp, PEPR = *Pentanisia prunelloides*, RHCO = *Rhynchosia cooperi*, SEBU = *Senecio bupleuroides*, SCCO = *Scabiosa columbaria*, SESP = *Senecio speciosa*, STNA = *Stachys natalensis*, TAOF = *Taraxacum officinale*, and VENA = *Vernonia natalensis*

Table 3.6: Summary of a partial redundancy analysis (pRDA) of the effect of grazing system (HDG vs LDG) on forb species composition (n = 40), after controlling for spatial variability, at Kokstad and Cedarville

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Kokstad				
Eigenvalue	0.114	0.122	0.079	0.038
Cumulative variation explained (%)[1]	21.36	44.24	58.97	66.01
Pseudo-canonical correlation	0.898			
Cedarville				
Eigenvalue	0.075	0.135	0.094	0.048
Cumulative variation explained (%)[1]	16.70	46.50	67.30	77.90
Pseudo-canonical correlation	0.698			

1Percentage of the residual variance accounted for after fitting covariables.

Table 3.7: Grass species percentage cover and forb species abundance (mean ± SE) for the species with at least 10% of their variation explained by grazing system in the pRDA, examined using a paired t-test (n = 20), for Kokstad and Cedarville sites. Grazing systems were high density, short duration stocking (HDG) and low density grazing (LDG)

Species	HDG	LDG	t	df	p
Kokstad					
Grasses					
Alloteropsis semialata	37.5 ± 2.21	23.4 ± 3.39	5.226	19	< 0.0001
Brachiaria serrata	3.2 ± 0.53	1.0 ± 0.29	3.694	19	0.002
Eragrostis curvula	2.8 ± 1.25	0.0 ± 0.00	2.207	19	0.040
Eragrostis plana	4.9 ± 1.31	0.8 ± 0.23	3.329	19	0.004
Hyparrhenia hirta	10.3 ± 4.27	24.1 ± 4.15	-3.029	19	0.007
Microchloa caffra	4.5 ± 1.67	0.5 ± 0.25	2.389	19	0.027
Themeda triandra	38.2 ± 2.38	46.5 ± 3.23	-2.888	19	0.009
Trachypogon spicatus	6.1 ± 2.03	15.7 ± 3.16	-4.326	19	< 0.001
Forbs					
Acalypha schinzii	3.53 ± 0.739	7.32 ± 0.655	-4.384	19	< 0.0001
Eriosema cordatum	2.02 ± 0.499	0.78 ± 0.416	3.134	19	0.005
Eriosema distinctum	0.00 ± 0.000	0.56 ± 0.161	-3.486	19	0.002
Eriospermum abyssinicum	0.01 ± 0.010	0.10 ± 0.034	-2.438	19	0.025
Gerbera ambigua	0.59 ± 0.153	0.22 ± 0.123	1.670	19	0.111
Helichrysum aureonitens	6.75 ± 0.536	10.86 ± 0.99	-4.119	19	0.001
Helichrysum herbaceum	0.84 ± 0.183	2.38 ± 0.352	-3.638	19	0.002
Pachycarpus sp.	0.10 ± 0.049	0.30 ± 0.065	-2.476	19	0.023
Pentanisia prunelloides	0.02 ± 0.014	0.37 ± 0.143	-2.544	19	0.020
Senecio bupleuroides	0.05 ± 0.029	0.99 ± 0.379	-2.508	19	0.021
Senecio speciosa	0.50 ± 0.093	0.02 ± 0.014	5.022	19	0.000
Stachys natalensis	0.24 ± 0.117	1.04 ± 0.329	-2.191	19	0.041
Taraxacum officinale	0.17 ± 0.052	0.02 ± 0.013	2.680	19	0.015
Cedarville					
Grasses					
Eragrostis capensis	2.0 ± 1.38	8.5 ± 2.44	-2.795	19	0.012
Themeda triandra	53.4 ± 2.39	48.0 ± 2.02	2.188	19	0.041
Forbs					

Commelina africana	0.90 ± 0.168	0.44 ± 0.114	2.632	19	0.016
Helichrysum aureonitens	5.72 ± 1.419	1.74 ± 0.492	3.030	19	0.007
Hermannia depressa	0.59 ± 0.249	1.91 ± 0.535	-2.142	19	0.045
Rhynchosia cooperi	0.36 ± 0.091	0.05 ± 0.025	3.490	19	0.002

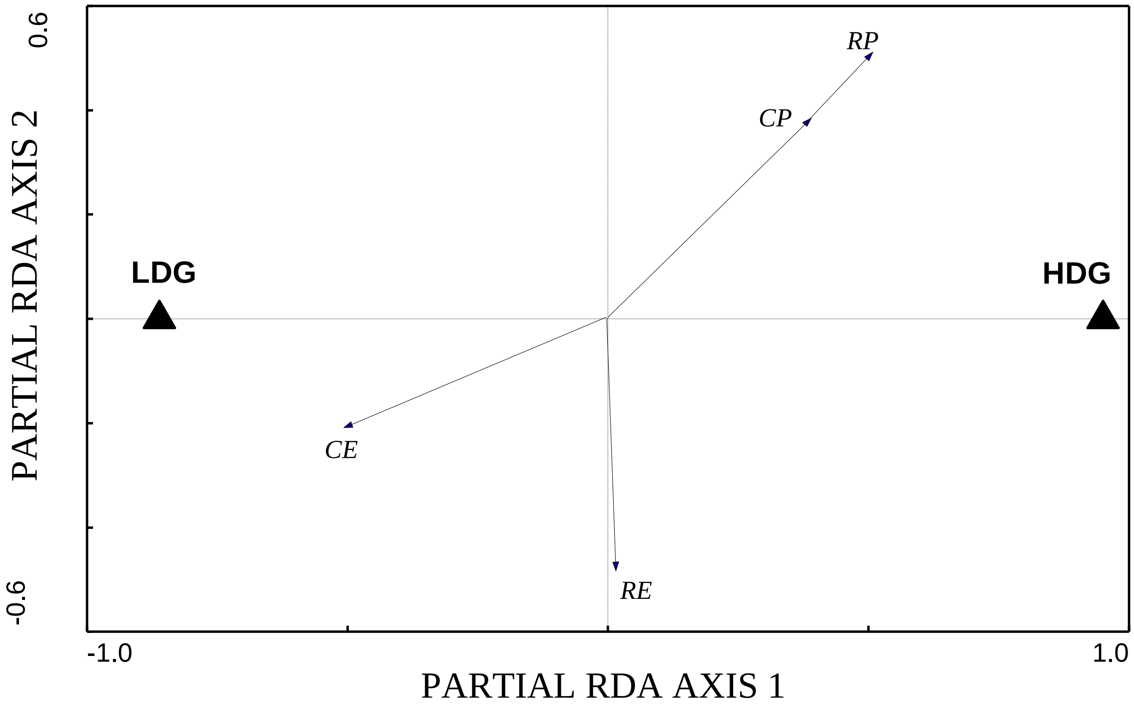

Figure 3.3: A partial redundancy analysis (pRDA) of the effect of grazing system (triangles), after accounting for spatial variability, on the proportion of forb species with different growth habits (represented by arrows) at Kokstad (n = 40). Grazing systems were: high density, short duration stocking (HDG) and low density stocking (LDG), and their difference accounted for 21.9% of the cumulative variance. Growth habits categories were: CE = cauline erect, CP = cauline prostrate, RE = radical erect and RP = radical prostrate.

3.5 Discussion

3.5.1 Impact of HDG on growing conditions for plants

Soil physical and chemical properties are important for plant growth and development; and for the maintenance of a healthy and stable ecosystem (Medina-Roldán et al. 2012). Contrary to the HDG claim that hoof action breaks the soil crusts without compacting the soil (Savory and Butterfield 2016), the soils were more compacted under HDG than LDG at both study sites. The intense trampling due to the higher stocking density under HDG may have resulted in the higher resistance to penetration for HDG compared to LDG. Compacted soils may reduce water infiltration into the soil and restrict plant root growth, which may result in some plants being easily uprooted by grazing (Donkor et al. 2002). The compacted soils under HDG may have resulted in some nutrients being lost through increased erosion (Pieper 1994) but the current study did not measure erosion. Soil chemical properties (total N, total C, pH) did not differ between HDG and LDG in either study site. This was again contrary to the HDG claim that large deposits of dung and urine increase soil nutrients (Savory and Parsons 1980, Savory and Butterfield 1999). Large deposits of dung and urine may increase soil nutrients, but the high concentration of animals may result in increased offtake of the nutrients as cattle consume plants and convert them into their biomass (Tiedemann et al. 1986, Frank et al. 1995). Therefore, although these nutrients may be returned to the soil, they may be taken off at a more rapid rate due to the high stocking rate in the HDG system. Alternatively, the rapid cycling of nutrients under HDG may have led to increased losses of nitrogen to the atmosphere via volatilisation (Bell et al. 2012).

HDG when compared to LDG increased litter mass at both study sites. High litter mass reduces evaporation from the soil surface and can increase water availability by improving infiltration (Larson and Whitman 1942). However, high litter accumulation can also reduce irradiation received by plants (Foster and Gross 1998) and limit growth and tillering from basal buds (Carson and Peterson 1990). Another detrimental effect of excessive litter on forbs is inhibition of seed germination and emergence (Facelli and Pickett 1991) as a consequence of suppressed germination cues and the physical difficulty of a new seedling breaking through dense litter (Foster and Gross 1998). A further indirect effect of litter accumulation in mesic grasslands may be a potential increase in fire temperatures at the soil surface if the litter is ignited (Prior et al. 2017), which may be detrimental to underground storage organs of forbs and buds at or just below the soil surface.

3.5.2 Impact of HDG on grass and forb species composition and diversity

3.5.2.1 Grasses

The use of small multiple paddocks under HDG and related grazing systems is contended to reduce the degree of selection by livestock (Teague et al. 2013). However, at Kokstad, HDG had a higher percentage cover of unpalatable species than palatable species compared to LDG, indicating that cattle were selecting for the palatable species. Differences observed in the current study compared to other long-term farm scale studies cited by Teague et al (2013) may be attributed to the differences in stocking rate. In the current study, HDG had a higher stocking rate compared to LDG, while in other farm-scale studies, all the compared grazing systems had the same stocking rate. Overstocking reduces the amount of time that a grass can be rested and increases the severity of defoliation, particularly on the preferred palatable species (Barnes 1992). Greater severity of defoliation means greater nutrient loss and greater root reduction, and therefore, a greater need for a longer rest to recover, which is not possible if the stocking rates are too high (Kirkman and Moore 1995).

Alternatively, the low percentage cover of palatable grass species may have been due to the absence of fire for >19 years. Most palatable species are vulnerable to shading by standing dead plant material and high litter accumulation while unpalatable species are less vulnerable (Everson et al. 1988, Fynn et al. 2011). Burning has also been shown to increase the tillering rate of some grasses on South African mesic grasslands (Everson et al. 1985) and on similar grasslands elsewhere (Collins and Gibson 1990, Morgan and Lunt 1999). In addition, fire is a uniform disturbance, hence it reduces the competitive advantage that the unpalatable species gain from not being highly selected for by cattle (Tainton and Mentis 1984). Similarly, the low response observed at Cedarville (difference in percentage cover on only two grass species) may possibly be an indication that fire is a necessity in the mesic grasslands and grazing cannot replace it (Uys et al. 2004).

3.5.2.2 Forbs

The high species turnover and low forb species abundance under HDG compared to LDG may possibly be due to the absence of fire under HDG at Kokstad. A similar but smaller response was observed at Cedarville were fire was excluded under both grazing systems. Fire plays a vital role in the development and growth of most South African mesic grassland forb species, as it stimulates resprouting and opens up space for them to establish (Bews 1925, Uys et al. 2004, Fynn et al. 2005). Observations in similar grasslands, tallgrass prairie in the United States of America (Freeman 1998) and temperate grasslands in Australia (Lunt and Morgan 2002), have also shown that most forb species in these grasslands are fire tolerant and that the exclusion of fire results in the replacement of these species by fire intolerant species.

Alternatively, the low forb species abundance under HDG may be due to the intense trampling impact associated with the high grazing pressure from the higher stocking rate and stocking density compared to LDG. Forbs with fleshy stems or leaves have been shown to be more susceptible to the trampling impact (O'Connor 2005, Uys 2006, Chamane et al. 2017). Although cattle do not generally select for forbs (Owen-Smith 1999), certain growth habits (e.g. tall statured forbs) are more exposed to cattle than others. Growing buds and leaf tissues of the erect growth habits are more exposed than those of prostrate forbs (Fynn et al. 2004). Forbs with erect growth habits decline with an increase in grazing pressure, whereas prostrate plants increase (Diaz et al. 2007). A similar trend was observed in the current study, where there was a decline of the cauline erect and an increase of the cauline prostrate and radical prostrate above-ground growth habits under HDG compared to LDG. These observations were in accordance with other South African mesic grassland studies that have shown that high grazing pressure results in either the loss of some forb species (O'Connor 2005, O'Connor et al. 2011, Scott-Shaw and Morris 2015) or a shift from long- to short-lived forbs (Uys 2006).

3.5 Conclusions

HDG potentially has long-term negative impacts on soil health and vegetation composition of South African mesic grassland. Soil compaction resulting from intense trampling under HDG may restrict plant root growth and may lead to reduced rainfall infiltration that may result in increased soil erosion. The intense grazing and trampling due to the higher stocking rate and stocking density under HDG resulted in the replacement of the cauline erect forb growth habit by the prostrate growth habit at Kokstad. The low percentage cover of desirable palatable grasses and the high forb species turnover under HDG at Kokstad coupled with the low grass and forb species responses at Cedarville indicate that fire may be indispensable and cannot simply be replaced by heavy grazing to maintain the structure, composition and productivity of mesic grasslands. That applies for both sustainable livestock production (Trollope 1999) and biodiversity conservation (Uys et al. 2004).

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CHAPTER 4: DOES HIGH-DENSITY STOKING AFFECT PERENNIAL FORBS IN MESIC GRASSLAND?

4.1 Abstract

Livestock production is an appropriate land use for mainstreaming biodiversity conservation, but little is known about the impact of grazing strategies on forbs that contribute most species, in grasslands. This study compared the effects of high-density, short-duration stocking (HDG) with no grazing (control) on vegetation structure, composition and demography of selected perennial forbs in a South African mesic grassland in a three-year experiment in KwaZulu-Natal, South Africa. HDG resulted in four-fold more and deeper litter accumulation, which reduced irradiance. Cover of three forb species, including the alien *Bidens pilosa*, was promoted and cover of another three forb species was reduced under HDG. There were no short-term effects of HDG on diversity, evenness and species richness. Ninety percent of forb species were damaged by HDG; type of damage varied widely from leaves and stems grazed to tearing and shredding by the hooves of cattle. Study of demography revealed that HDG threatened future populations of the grazing-sensitive species *Afroaster hispida, Agathisanthemum chlorophyllum* and *Gerbera ambigua* through increased mortality or reduction in the recruitment of large from small individuals. This study has revealed that HDG potentially has negative direct and indirect effects on indigenous perennial forbs in a South African mesic grassland.

Keywords*: biodiversity conservation, population dynamics, short-duration grazing*

4.2 Introduction

Historically, the main aim of grassland management in South Africa had been sustainable production of livestock (Tainton 1999). Over the past decade, livestock production systems have been identified as one of the most appropriate land uses for mainstreaming biodiversity conservation in grassland (O’Connor and Kuyler 2009). Mainstreaming biodiversity conservation means including or making biodiversity conservation part of livestock production systems. However, research on extensive livestock production on rangelands has traditionally focused on grasses because they contribute the most of the available forage for livestock (Tainton 1999). In contrast, the numerous forb species (herbaceous dicotyledons and non-graminoid monocotyledons), which comprise most of the species in mesic grassland (Bullock et al. 2001, Morris 2004), have been largely ignored (O’Connor et al. 2010). High plant diversity maintains ecosystem functioning and delivery of services in response to disturbance through the insurance of functional redundancy (Frank and McNaughton 1991, Tilman and Downing 1996), thus improved understanding of livestock impact on forb diversity is required.

Mesic grassland forbs are mainly long-lived perennials that regenerate annually in spring from underground storage organs such as bulbs, rhizomes, corms or tubers (Bews 1925, Bond and Parr 2010, Carbutt et al. 2011). The existence of these forbs is dependent on fire to maintain an open habitat and stimulate resprouting (Bews 1925, Fynn et al. 2004, Uys et al. 2004, Bond and Parr 2010). Their ability to resprout from an underground organ enables them to withstand moderate grazing (Uys 2006). Limited studies in South African mesic grassland have shown that high grazing pressure results in the loss of forb species (O'Connor 2005, O'Connor et al. 2011, Scott-Shaw and Morris 2015) or in a shift from long- to short-lived forbs (Uys 2006). However, information on the direct and indirect effects of different grazing management strategies and components thereof on forb species composition and persistence of individual species is sparse for South African mesic grasslands.

High-density, short-duration stocking (HDG) is a popular grazing system in South African mesic grassland (Skovlin 1987, Zietsman 2010, Phillips 2014). Claimed benefits of HDG include higher stocking rates contended to result in greater profit (Savory and Parsons 1980, Savory and Butterfield 2016). Under HDG, grazing can occur at very high densities on small areas for limited durations resulting in temporary high densities far in excess of other grazing strategies (O'Connor et al. 2010). The resulting high stocking density is viewed as essential to HDG as it creates a 'herd effect' with the intent to minimise selective grazing and more completely utilise herbage on offer. Biomass that is not grazed is trampled, purportedly promoting incorporation of plant material into the soil, increasing rates of nutrient cycling, and increasing overall plant productivity (Savory and Parsons 1980, Savory 1983, 1988). Fire is not applied in this grazing method to allow litter to accumulate for protecting soil moisture, increasing rainfall infiltration and reducing soil erosion (Savory 1983). HDG practitioners claim that the overall condition of the veld, including plant species diversity, can be improved by this grazing strategy (Savory and Parsons 1980, Zietsman 2010, Savory and Butterfield 2016). There is, however, no empirical evidence in support of these claims for mesic grasslands in South Africa.

Grazing exerts indirect effects on a grass sward through its influence on the abiotic environment, especially irradiance, by altering sward structure (Archer and Smeins 1991). A further potential indirect impact of heavy grazing pressure on forbs is alteration of the competitive interaction between forbs and grass as a consequence of grass, not forbs, decreasing in volume and abundance due to defoliation (Fahnestock and Knapp 1994, Hartnett et al. 1996).

Mesic grasslands are highly productive because of high rainfall (>600 mm per annum) (Palmer and Ainslie 2005). Hence, the exclusion of fire under HDG may result in substantial accumulation of litter (Heady et al. 1992). This build-up of litter may suppress plant production and decrease the abundance and cover of some plants, especially forbs (Carson and Peterson 1990, Hayes and Holl 2003), thereby reducing plant species richness, in part because of reduced irradiance.

Direct impact on forbs resulting from heavy grazing pressure on above-ground biomass may include tearing and shredding from trampling, and defoliation of leaves, stems and reproductive organs from grazing (Huntly 1991). This impact may affect the vigour and reproduction potential of a plant and may result in its mortality. Above-ground biomass removal and trampling by livestock under HDG may be extensive, resulting in the loss of some grazing-sensitive forb species, while favouring more grazing- and trampling-resistant forbs as well as alien weed species (O’Connor 2005). A pronounced impact of HDG on forbs through trampling or grazing is expected owing to high stocking density, especially early in the growing season when most forb species are actively growing.

Compositional change is a consequence of population changes of individual species, particularly of the most abundant and dominant species (Williams 1970, O’Connor 1994). In South Africa, understanding of population response to grazing has been focused on grasses (O’Connor and Everson 1998) but not forbs. Such an understanding is required for maintaining the forb component in grazed systems, which would usually include both grazing-sensitive and grazing-tolerant species (Scott-Shaw and Morris 2015).

The aim of this study was to compare the short-term impact of HDG with no grazing (control) on vegetation structure and composition, forb abundance and demography in a South African mesic grassland. ‘No grazing’ offered a more absolute comparison than would have been obtained with comparison with a prevailing formal system as the latter is highly variable among users. However, in order to gain insight into HDG versus ‘conventional grazing systems’, this study was complemented by a separate study comparing HDG with ‘real world’ conventional grazing systems using fence-line contrasts (Chamane et al. 2016). The following specific questions were addressed:

- Under HDG, is vegetation cover, litter and grass phytomass altered to an extent that they may affect the growth of forbs?
- Can HDG affect plant species composition, diversity and abundance over the short term?

- What is the range of impact of HDG across species and does this depend on season or on inter-annual differences?
- Does HDG have an effect on mortality, change in size or regeneration of either grazing-tolerant or grazing sensitive forb species?

4.3 Materials and methods

4.3.1 Study area

The study was located at Ukulinga Research Farm (29°39′58.42″ S, 30°24′04.6245″ E) of the University of KwaZulu-Natal, South Africa. Mean annual precipitation is 735 mm (CV 15%), falling mainly over the summer growing season (October–April). Summers are warm to hot with a mean monthly maximum of 26.4 °C in February and winters are dry and cool with occasional frost and a mean monthly minimum of 8.8 °C in July. The experimental area was situated on a plateau at an altitude of 840 m above sea level. The soils are acidic and are classified as Westleigh and Mispah forms derived mostly from Ecca group shale of the Karoo sedimentary sequence (Soil Classification Working Group 1991). The closed canopy, forb-rich grassland is classified as Moist Midlands Mistbelt Grassland (Mucina et al. 2006). The farm was established in 1948 and the grasslands for this study have subsequently been used for livestock grazing at low stocking rates.

4.3.2 Experimental design

The study was conducted in good-condition grassland with minimal bare soil, dominated by productive palatable perennial grasses such as *Tristachya leucothrix*, *Themeda triandra* and *Eragrostis curvula* and a large number of forb species (Foran et al. 1978). Good-condition grassland was selected in order to ensure that treatment effects would not be obscured by initial grassland state. Five 0.25 ha paired (one treatment, one control) paddocks were established. Two paired plots were on grassland that was regularly grazed and burned every 2–3 years, two were on grassland that had been grazed, burnt and occasionally mowed in recent years, and one was in grassland that had been regularly mowed for hay production, with no grazing or burning. For the duration of the study, all the control paddocks were ungrazed and were burned once late in the dormant season (August 2014). Simulated high-density, short-duration stocking (HDG) was applied on the treatment paddocks. The HDG stocking density applied was 60 cattle ha−1 per paddock for 2–4 d followed by a 60-day rest period, which is a HDG stocking density generally used in South African mesic grassland (P Ardington, HDG practitioner, pers. comm., 2012). The average size of the cattle used in the grazing treatment was 350 kg. Stocking was applied early (October–January) and late (February–April) in the growing season for a period of three growing seasons (2013/14, 2014/15 and 2015/16). The institutional and national guidelines for the care and use of animals were followed: the ethical clearance reference was AREC/009/016D.

4.3.3 Vegetation structure

Ten 40 m transects were laid out at approximately equal intervals per paddock to measure ground cover using a point intercept method (Naeth et al. 1991) in April 2016. A sampling pole with a 3-mm-diameter pin was dropped down every 0.5 m along each transect to total 80 points per transect. Ground-cover types recorded were live vegetation, bare soil, rock or litter. Live vegetation was recorded as struck when the point of a pin touched the base of a plant.

Litter, defined as dead detached plant material on the soil surface, and standing phytomass were measured in 20 randomly placed 0.25 m^2 quadrats in each paddock at the end of the experiment. Litter depth was sampled by pushing a 3 mm pin through the litter to the soil surface and measuring the highest horizontal dead-plant material (Hayes and Holl 2003). Litter biomass was collected from each quadrat. Standing phytomass was clipped to the ground surface and separated into grass and forbs. Litter mass and standing phytomass were oven dried at 60 °C for 72 h and then weighed.

4.3.4 Vegetation composition and livestock impact

Twenty-five 0.25 m^2 quadrats were randomly located and tagged, using wire pegs inserted into the ground, in each of the five paired paddocks to measure plant species abundance and immediate HDG impact on forb species. The measurements were recorded early and late in the growing season for a period of three growing seasons (2013/14, 2014/15 and 2015/16). For plant species abundance, each time before treatment, the percentage cover of each plant species rooted in the quadrat was visually estimated to the nearest 5% (Burns et al. 2009). For HDG impact on forbs, immediately after treatment, the proportion of the above-ground plant volume removed by grazing (cleanly removed presumably by cattle) or damaged by trampling (leaves and/or stem torn and shredded) was estimated to the nearest 10% per forb species per quadrat (Ehrlen 1995). Nomenclature of all plant species follows the South African National Biodiversity Institute Database (SANBI 2015).

4.3.5 Population dynamics

The effect of HDG on the growth, mortality and reproduction of four abundant perennial forb species was investigated using size classes. Mortality was defined as the disappearance of above-ground biomass and the underground storage organ may or may not have persisted. Species were selected to include decreasers, which were *Afroaster hispida*, *Agathisanthemum chlorophyllum* and *Gerbera ambigua*, and an increaser *Spermacoce natalensis* (Scott-Shaw and Morris 2015).

Individuals of these four forb species (20 individuals per species per paddock) were tagged using coloured wire and mapped in order to ensure relocation of individuals. An individual was defined as a discrete cluster of stems and an apparently independent unit, separated from other stems by at least 10 cm (Angert 2006). Measurements of plant height (cm) and basal diameter (mm) were taken early in the growing season (January 2014 and January 2015).

Plant size is a better indicator than age for study of a population response in terms of growth, mortality and reproduction (Harper 1977, Caswell 2001, Fienberg 2007). Basal diameter is a more useful index of plant size than plant height and number of stems/leaves (Reppert et al. 1963). Therefore, basal diameter (mm) was used to derive size classes in order to examine the demographic fate of individuals of each species (O’Connor 1993, 1994, Caswell 2001). Four categories of demographic fate were defined for the transition period from January 2014 to January 2015. An individual could (1) die, (2) decline in size, (3) remain the same size or (4) increase in size. Size classes or states were represented as 0 = dead, 1 = 1 mm, 2 = 2 mm and 3 for ≥3 mm basal diameter. Due to insufficient sample size, some size classes were amalgamated in a species-specific manner. For *Afroaster hispida*, size classes 2 and 3 were combined to form size class 2/3. For *Gerbera ambigua* and *Spermacoce natalensis,* size classes 1 and 2 were combined to form size class 1/2.

4.3.6 Statistical analysis

A paired *t*-test ($n = 5$) was used to analyse whether ground-cover categories (bare ground, live vegetation and litter) and plant species diversity differed between HDG and the control. A fire in one HDG plot in 2015 reduced the sample size for assessing treatment effects on components of phytomass. Therefore, a nested analysis of variance (treatment nested within location) was used to analyse whether litter mass, standing grass and forb phytomass differed between HDG and the control, with the variables appropriately transformed to minimise the skewness and heteroscedasticity of residuals. Diversity was expressed as (1) Shannon–Wiener diversity index (*H*′), (2) Pielou's evenness (*J*′) and (3) species richness (*S*) (Magurran 2004). Data used to calculate *H*′ and *J*′ were the species percentage cover from the last early growing season (2015/16) expressed per m^2 per paddock. Species richness was the number of grass and forb species per m^2, assessed from a total area of 6.25 m^2 from 25 quadrats per paddock.

Partial canonical correspondence analysis (pCCA), a direct gradient technique, was used to examine whether treatment (HDG vs ungrazed control), season (early vs late growing season), year (2013/14, 2014/15 and 2015/16) and the interaction between treatment and year accounted for the pattern of compositional variation (plant species percentage cover) using Canoco version 4.56 (ter Braak 2009). Differences among the five paired site locations were partialled out in order to account for spatial variation in composition. A Monte Carlo permutation test (999 permutations) was used to test the significance of the fitted variables. Species that only appeared once were excluded from the analysis. Correspondence analysis was chosen because there was a high species turnover.

Patterns of damage across species in the grazed plots were assessed with a pCCA to examine whether year, season and the interaction between year and season accounted for variation in percentage damage to forbs by grazing and trampling, with year and season defined as above.

An effect of HDG versus control on population processes was tested separately for each species. Mortality was examined using a chi-square or Fischer's test depending on data properties. Size class transitions were examined using contingency tests provided there was sufficient representation of size classes, which excluded *S. natalensis* and *A. chlorophyllum*.

4.4 Results

4.4.1 Vegetation structure, composition and livestock impact

HDG compared with an ungrazed control supported 1.7 times less grass phytomass, three-fold greater litter cover which was four-fold deeper, a similar amount of forb phytomass, slightly less cover of live vegetation, and half the amount of bare ground (Table 4.1).

A total of 130 plant species were recorded in 10 paddocks; 18 were grasses and 112 were forbs of which 95 were dicotyledons and 17 were monocotyledons (Table 4.2). Of the 112 forb species, 22 were Asteraceae, 18 were Fabaceae and the remainder were spread across 28 other families. There were no short-term effects of HDG on *H*′, *J*′ or *S* (Table 4.3). The pCCA indicated that grazing treatment accounted for a small, but significant, amount of compositional variation along the first axis (pseudo-*F* = 3.1, *p* = 0.003) and for the ordination overall (pseudo-*F* = 1.7, *p* = 0.036). Year (pseudo-*F* = 1.6, *p* = 0.055) had a marginal effect whereas season (pseudo-*F* = 1, *p* = 0.463) and interaction between treatment and year (pseudo-*F* = 0.8, *p* = 0.614) had no effect on compositional variation. Axis 1 was defined primarily by treatment (Figure 4.1) and accounted for 5.8% of the 11.8% total variation explained. The species whose variance was well accounted for by the pCCA for the treatment were mainly those whose abundance differed significantly between HDG and the control (Table 4.4). Of the 69 species tested, HDG promoted the forb species *Bidens pilosa*, *Pachycarpus* sp. and *Senecio retrorsus*, but reduced the percentage cover of the grass *Brachiaria serrata* and of the forbs *Corchorus asplenifolius*, *Eriosema cordatum* and *Helichrysum miconiifolium* (Table 4.4).

Ninety-two of 102 forb species were damaged under HDG over three growing periods. The majority of individual forb plants, irrespective of species, experienced HDG damage and only 7% were not damaged. Of those damaged, most experienced an intermediate (10–50% biomass lost) level of damage, whereas 10% lost more than 50% per individual (Figure 4.2). A damage level of <20% was experienced only by infrequent species, whereas all abundant species experienced substantial damage (Figure 4.3). However, a number of uncommon species (<5% occurrence) suffered the highest level of damage (Figure 4.3). Damage patterns under HDG did not vary between seasons (pseudo-*F* = 1, *p* = 0.435) or over years (pseudo-*F* = 1.3, *p* = 0.18), nor was the interaction between season and year significant (pseudo-*F* = 0.8, *p* = 0.722). Therefore, differences in damage are presumably related to intrinsic differences among species. *Afroaster hispida* and *Spermacoce natalensis* endured more grazing impact than trampling impact, whereas *Gerbera ambigua* (Table 4.5) and *Agathisanthemum chlorophyllum* endured more trampling than grazing. No analysis was conducted for *A. chlorophyllum* because of insufficient sample size.

Table 4.1: Treatment differences (mean ± SE) between high-density, short-duration stocking (HDG) and an ungrazed control examined using nested analysis of variance for standing grass and forb phytomass and litter mass (*n* = 4); and a paired *t*-test of litter depth and percentage cover for each of bare ground, live vegetation and litter at Ukulinga Research Farm of the University of KwaZulu-Natal (*n* = 5)

Variable	HDG	Control	F	P
Grass phytomass (g m^{-2})	164.8±10.89	287.1±13.13	29.19	<0.001
Forb phytomass (g m^{-2})	29.8±3.64	35.0±4.25	1.15	0.337
Litter mass (g m^{-2})	54.7±5.04	14.6±1.20	54.84	<0.001
Variable	HDG	Control	t	P
Litter depth (cm)	2.0±0.86	0.5±0.420	4.21	0.025
Litter cover (%)	37.4±7.74	11.0±3.49	5.24	0.006
Live vegetation (%)	42.0±4.16	51.4±1.50	-2.64	0.057
Bare ground (%)	19.0±5.57	36.8±3.67	-4.72	0.009

Table 4.2: Dominant species, their growth habit, palatability to cattle and frequency of occurrence within twenty-five 0.25 m2 quadrats on the five paired paddocks before the onset of the experiment (October 2013) at Ukulinga Research Farm of the University of KwaZulu-Natal

Species names	Frequency (%)	Growth habit	Palatibility
Grasses			
Tristachya leucothrix	53.8	Bunch grass	Palatable
Themeda triandra	46.1	Bunch grass	Palatable
Eragrostis curvula	25.4	Bunch grass	Unpalatable
Setaria sphacelata	22.1	Bunch grass	Palatable
Forbs			
Gerbera ambigua	19.4	Prostrate, leaves are large, thinly hairy and white underneath	Unknown
Eriosema cordatum	14.6	Prostrate, covered with loose reddish hairs, leaves are large and few	Unknown
Senecio coronatus	14.6	Erect, has several leafy flowering stems	Unknown
Afroaster hispida	14.4	Erect, stem and leaves hairy with purple flower	Unknown

Table 4.3: Shannon–Wiener diversity index, Pielou’s evenness and total species richness for high-density, short-duration stocking (HDG) and control (mean ± SE) examined using a paired *t*-test (*n* = 5) at Ukulinga Research Farm of the University of KwaZulu-Natal

Index	HDG	Control	t	P
Shannon diversity index (m^{-2})	2.8±0.12	2.8±0.14	0.611	0.574
Pielou’s evenness (m^{-2})	0.6±0.24	0.6±0.03	0.611	0.574
Richness (m^{-2})	6.2±0.18	6.7±0.23	-0.712	0.516

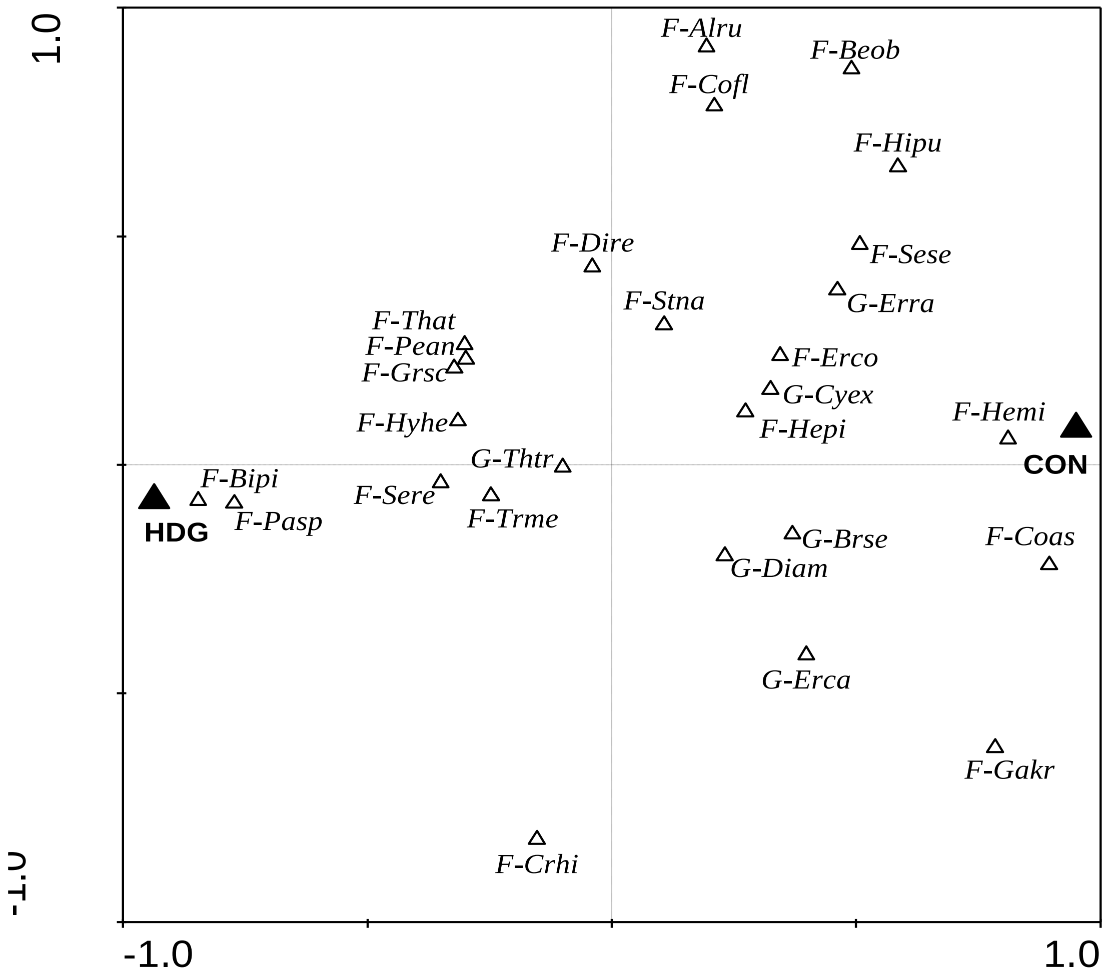

Figure 4.1: Canonical correspondence analysis plot of centroids for plant species percent cover between short-duration, high-density stocking (HDG) and ungrazed control (CON) for six sampling seasons at Ukulinga Research Farm of the University of KwaZulu-Natal. Only species with at least 5% variation explained are shown. Grey triangles represent species. G = grass: Brse, *Brachiaria serrata*; Cyex, *Cymbopogon excavatus*; Diam, *Diheteropogon amplectens*; Erca, *Eragrostis capensis*; Erra, *Eragrostis racemosa*; Thtr, *Themeda triandra*; F = forb: Alru, *Alysicarpus rugosus*; Beob, *Becium obovatum*; Bipi, *Bidens pilosa*; Coas, *Corchorus asplenifolia*; Cofl, *Conyza floribunda*; Crhi, *Crabbea hirsuta*; Dire, *Diclis reptans*; Erco, *Eriosema cordatum*; Gakr, *Gazania krebsiana*; Grsc, *Graderia scabra*; Hemi, *Helichrysum miconiifolium*; Hepi, *Helichrysum pilosellum*; Hipu, *Hibiscus pusillus*; Hyhe, *Hypoxis hemerocallidea*; Pasp, *Pachycarpus* sp.; Pean, *Pentanisia angustifolia*; Sere, *Senecio retrorsus*; Sese, *Sebaea sedoides*; That, *Thunbergia atriplicifolia*; Trme, *Tragia meyeriana*

Table 4.4: Plant species percentage cover (mean ± SE) for high density, short duration stocking (HDG) and ungrazed control examined using a paired *t*-test ($n = 5$) over six sampling occasions at Ukulinga Research Farm of the University of KwaZulu-Natal

Plant species	HDG	Control	t	p
Brachiaria serrata	1.3±0.12	2.8±0.31	7.59	0.0006
Bidens pilosa	0.8±0.13	0.04±0.015	5.07	0.0039
Corchorus asplenifolius	0.01±0.01	0.2±0.04	5.12	0.0037
Eriosema cordatum	0.9±0.09	1.9±0.26	4.48	0.0065
Helichrysum miconiifolium	0.01±0.013	0.2±0.02	7.14	0.0008
Pachycarpus sp.	0.3±0.04	0.03±0.013	6.78	0.0011
Senecio retrorsus	1.0±0.07	0.5±0.05	6.74	0.0011

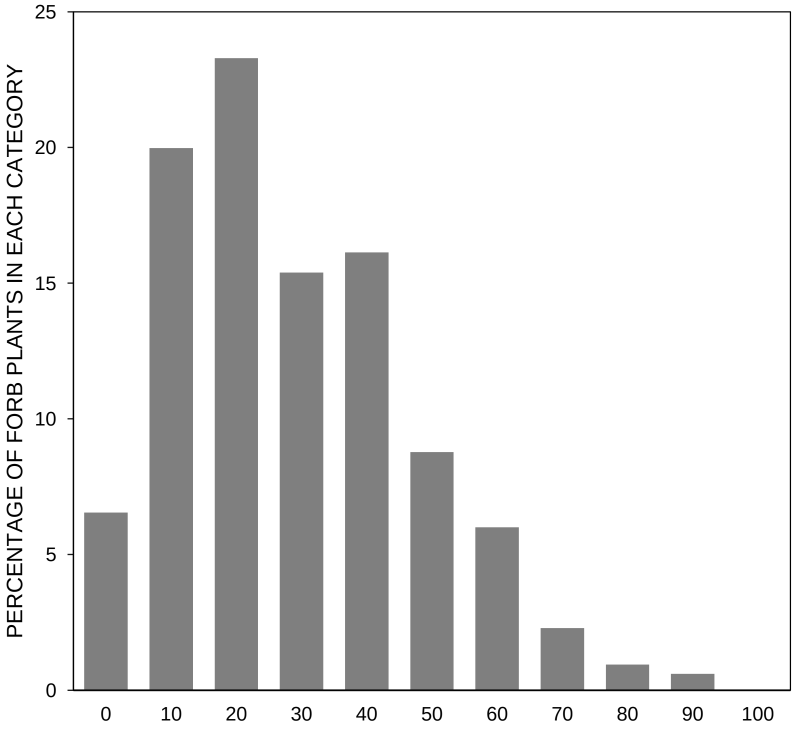

Figure 4.2: Percentage of forb plants (irrespective of species) for the high-density, short-duration stocking paddocks in each damage category (percentage loss of above-ground biomass) over six sampling occasions at Ukulinga Research Farm of the University of KwaZulu-Natal

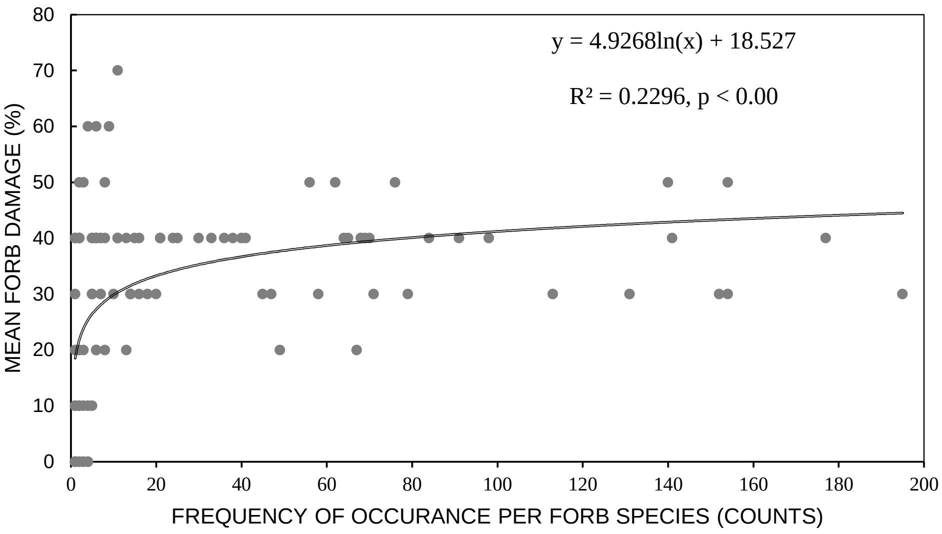

Figure 4.3: Scatter plot of percentage damage versus frequency of occurrence (counts) per forb species in 750 quadrats (25 quadrats in five paddocks over six sampling occasions under high-density, short-duration stocking at Ukulinga Research Farm of the University of KwaZulu-Natal

Table 4.5: Grazed vs trampled percentage damage (mean ± SE) under high-density, short-duration stocking for Afroaster hispida, Gerbera ambigua and Spermacoce natalensis over six sampling occasions at Ukulinga Research Farm of the University of KwaZulu-Natal (n = 5)

Plant species	Grazed	Trampled	t	p
Afroaster *hispida*	34.0 ± 2.44	8.0 ±2.00	6.5	0.003
Gerbera ambigua	10.0 ± 0.00	22 ± 2.00	-6.0	0.004
Spermacoce natalensis	30 ± 3.16	6 ± 2.44	9.8	0.001

4.4.2 Population dynamics of selected forb species

HDG resulted in escalated mortality of the two decreaser species *Afroaster hispida* and *Agathisanthemum chlorophyllum* as well as the increaser species *Spermacoce natalensis*, but had no influence on mortality of the decreaser *Gerbera ambigua* (Figure 4.4, Table 4.6). HDG further had a conspicuous effect on transitions between size classes for *A. hispida* ($\chi2 = 39.35$, $p < 0.0001$), *A. chlorophyllum*, *G. ambigua* ($\chi2 = 39.91$, $p < 0.0001$) and *S. natalensis* (Figure 4.4). However, there was insufficient sample size to construct size class transitions for *A.*

chlorophyllum and *S. natalensis*. The effect of HDG was to both constrain recruitment of large from small individuals as well as to reduce individual size for the decreasers *A. hispida* and *G. ambigua*, but these effects were not apparent for the increaser *S. natalensis* (Figure 4.4). Therefore, in general, decreaser species under HDG experienced increased mortality, reduced growth and even a decline in individual size. By contrast, the single increaser species also experienced increased mortality under HDG, but individual growth was relatively unaffected.

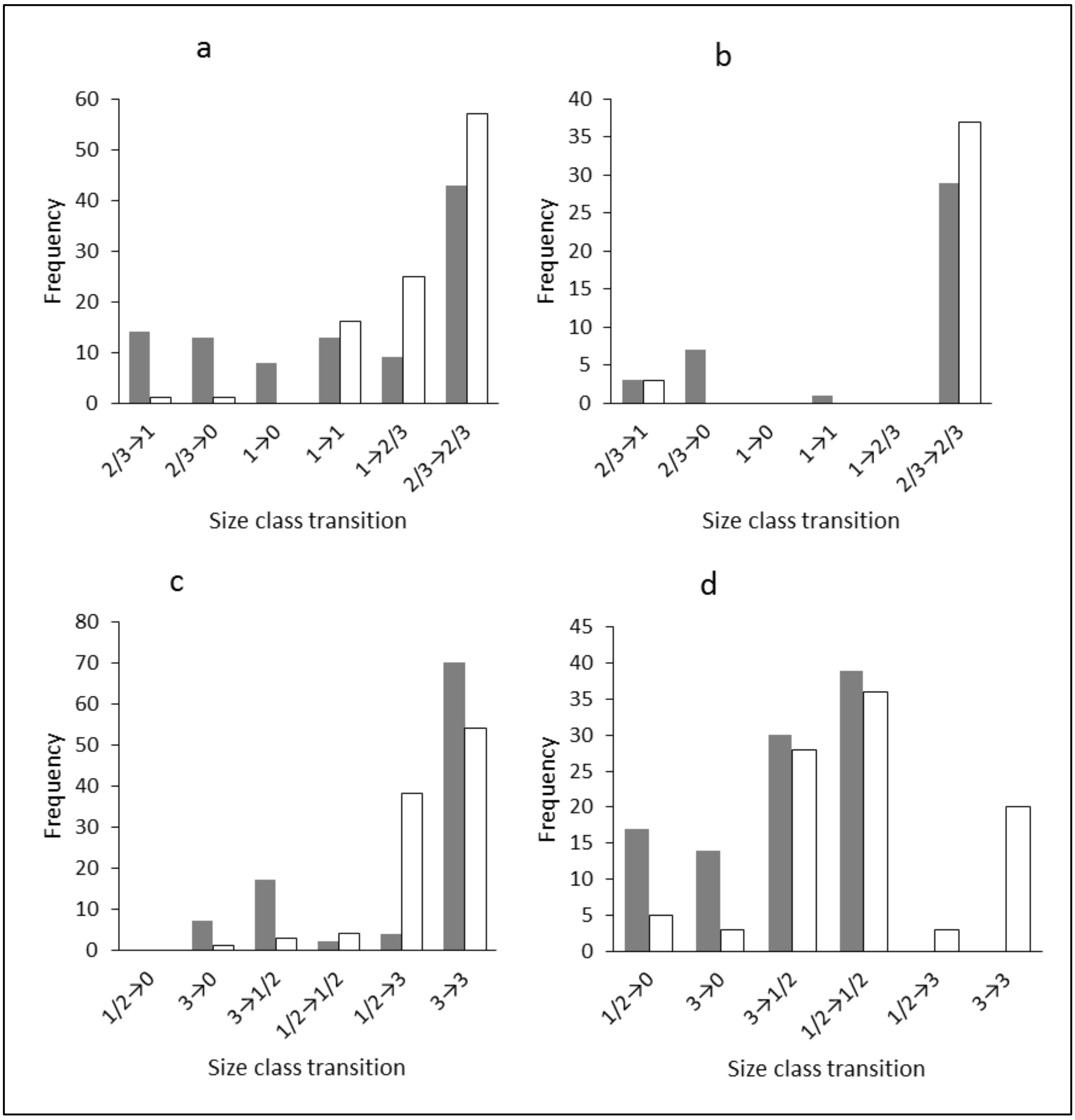

Figure 4.4: Transition between size classes for January 2014–January 2015 based on basal diameter for *Afroaster hispida* (a), *Agathisanthemum chlorophyllum* (b), *Gerbera ambigua* (c) and *Spermacoce natalensis* (d) in a South African mesic grassland at Ukulinga Research Farm

of the University of KwaZulu-Natal. Dark grey bars represent frequency of the size class transition under high-density, short-duration stocking, and pale grey bars represent frequency of the size class transition under no grazing (*n* = 100 for each species per treatment except for *Agathisanthemum chlorophyllum* for which *n* = 40)

Table 4.6: Fate (alive or dead) of individuals under high-density, short-duration stocking (HDG) and ungrazed control from January 2014 to January 2015 for *Afroaster hispida*, *Agathisanthemum chlorophyllum*, *Gerbera ambigua* and *Spermacoce natalensis* at Ukulinga Research Farm of the University of KwaZulu-Natal. Sample sizes are in parentheses

Treatment	**Fate of *Afroaster***					**Fate of *Agathisanthemum***				
	Alive	Dead	Total	χ^2	P	Alive	Dead	Total	χ^2	P
HDG	79(79)	21(21)	100			82.5(33)	17.5(7)	100		
Control	99(99)	1(1)	100			100(40)	0(0)	100		
Total	89(178)	11(22)	(200)	20.43	<0.0001	91(73)	9(7)	(195)	7.67	0.006
Treatment	**Fate of *Gerbera***					**Fate of *Spermacoce***				
	Alive	Dead	Total	χ^2	P	Alive	Dead	Total	χ^2	P
HDG	93(93)	7(7)	100			69(69)	31(31)	100		
Control	99(99)	1(1)	100			92(87)	8(8)	100		
Total	96(192)	4(8)	(200)	4.69	0.065	80(156)	20(39)	(195)	15.52	<0.0001

4.4 Discussion

4.4.1Direct versus indirect impacts of HDG on forbs

HDG predictably reduced grass phytomass of the mesic grassland study site, which was dominated by palatable grass species such as *Themeda triandra* and *Tristachya leucothrix.* A possible response was for forb phytomass to increase under HDG owing to competitive release resulting from reduced grass phytomass but this was not observed. Failure of forbs to benefit from a reduction in grass phytomass may be attributed to pronounced direct negative effects of HDG on them. Almost all (90%) of forb species were physically damaged by livestock under HDG (Figure 4.3), with a modal biomass loss of 20% (Figure 4.2), and with type of damage ranging from leaves bitten off to partial or whole tearing and shredding of leaves and stems. Other principal vegetation impacts of HDG were a reduction of live vegetation cover and the development of a thick, heavy layer of litter (Table 4.1). A solid ground litter cover increases water availability by improving water infiltration and reducing evaporation from the soil surface (Larson and Whitman 1942), which should promote vegetation growth. However, high litter cover may reduce irradiation, received by especially low-statured plants (Foster and Gross 1998), further hindering their growth and likely ultimately resulting in their mortality (Bews 1925, Carson and Peterson 1990).

4.4.2 Population responses of forbs to HDG

HDG exerted variable effects on the demography of the four forb species studied. A consistent trend for the decreaser species under HDG was an increase in mortality for *Afroaster hispida* and *Agathisanthemum chlorophyllum*; and a decline in the recruitment of small to a larger size class for *Afroaster hispida* and *Gerbera ambigua* indicating these species may be vulnerable. *Agathisanthemum chlorophyllum* persisted mainly as a large size class and was susceptible to HDG impact; due to its fleshy stems and leaves, it experienced high trampling impact that may have increased its mortality. These findings are consistent with those of another study in South African mesic grassland in which *Agathisanthemum chlorophyllum* became locally extirpated under sustained heavy grazing (Scott-Shaw and Morris 2015). For *Afroaster hispida*, all size classes were negatively affected under HDG, including increased mortality irrespective of size class. It was observed that cattle grazed *Afroaster hispida*, as the majority of plants had leaves and stems cleanly removed as opposed to being trampled, with leaves and stems being torn or shredded. *Afroaster hispida* may have been more susceptible to grazing due to its erect growth habit that rendered plants more apparent and accessible to cattle. A similar response was observed in an American tallgrass prairie where high-intensity grazing reduced shoot biomass and height of *Aster ericoides*, which has a similar growth habit to *Afroaster hispida* (Hickman and Hartnett 2002). Mortality of *Gerbera ambigua* was not affected by HDG, either because it is possibly unpalatable or inaccessible to livestock because of its prostrate growth form, i.e. <5 cm tall (Cid and Brizuela 1998). However, the soft stem and the soft broad leaves of the small size class may have made it more susceptible to trampling under HDG, which may have resulted in a decline in the recruitment of the small to the large size class. HDG increased the mortality of *Spermacoce natalensis* (Table 4.5), which is susceptible to being grazed because of its erect growth habit, a feature shared with *Afroaster hispida*. However, future populations under HDG are potentially not under threat because the small size class through which it persisted was unaffected (Figure 4.4). Similarly, a study in the South African mesic grassland that has a long history of grazing (>10 years) showed that *Spermacoce natalensis* was more abundant under severe grazing, whereas *Afroaster hispida* and *G. ambigua* declined drastically under severe grazing (Scott-Shaw and Morris 2015). The findings of this study, although short-term, have shown that more forb species of this mesic grassland are unlikely adapted to high grazing pressure.

4.4.3 Assessing impact of grazing systems on forb diversity

The inability to detect treatment differences using diversity indices (*S*, *H′* and *J′*) may be due to the short-term nature of the study. Alternatively, it may be the inability of these indices to reflect changes in diversity resulting from species shifts, such as a grazing-induced shift from perennial to alien or annual species. No differences were observed in plant species percentage cover between the early and late growing season over a period of three growing seasons under HDG, but changes may become evident over a longer period (e.g. SC unpublished data). However, HDG affected the abundance of at least six forb species, with three increasing and three decreasing over the short time of the study. Two of the three forb species that were promoted under HDG are recognised problem plants. *Bidens pilosa* is an alien weed and *Senecio retrorsus* can be poisonous to livestock when consumed in large quantities (Tainton 1972). The three forb species that declined under HDG may have been susceptible to high grazing pressure and trampling due to their fleshy stems and erect growth habits. These short-term changes in the abundance of species can translate into shifts in species composition over time (Uys 2006). In the South African mesic grasslands, long-lived perennials subjected to sustained grazing pressure may be replaced in part by hardy annual and alien species (Tainton 1972, Scott-Shaw and Morris 2015). Hence to understand grazing impacts on plant diversity, appropriate functional groups (Diaz et al. 2007) need to be identified rather than using diversity indices. Identification of functional groups in South African grassland is in its infancy, other than simple classification according to growth or life form (Uys 2006, Scott-Shaw and Morris 2008). Identification of functional groups or forbs would need to take into account the presence and nature of underground storage organs. As their use could contribute to providing insight for mainstreaming conservation of plant diversity into livestock production systems, development of functional groups of forbs within South African grasslands emerges as a priority.

4.4.4 Can forb diversity be maintained under HDG?

A number of lines of evidence became apparent during this short-term study that raise concern about maintaining forb diversity under HDG. First, two of three species considered as grazing-sensitive experienced increased mortality and reduced growth within only two seasons of HDG treatment (see section Population responses of forbs to HDG). However, in the short-term (<10 years) this may be reversible because, although individuals of these forbs appear to be dead, their underground storage organs may still be alive (Fynn et al. 2004, Uys et al. 2004, Uys 2006) and growth might be revived if fire is re-introduced soon enough. Second, the general relationship across 102 species was that the more abundant species were more severely damaged and some of the most uncommon species were either the most severely damaged or effectively undamaged under HDG (Figure 4.3). The observed variation in species response to livestock impact may be due to the different species traits, for example, tall-statured forbs may be more apparent, and if palatable, would be selected for, whereas forbs with fleshy stems or leaves may be susceptible to the trampling impact (as shown in the section Population responses of forbs to HDG). It concurs with other studies done on tallgrass prairie, which showed that variation in plant traits such as growth form, palatability and local abundance all influence the impact of herbivores on forbs (Hartnett et al. 1996, Hickman et al. 2004). Contrary to what was expected, forb damage did not vary between the early growing and late growing season possibly because HDG impact on forbs may have been more influenced by the variation in plant species traits rather than temporal variations. These observations indicate that mesic grassland forbs may not be adapted to high grazing pressure and the continuation of HDG may result in these species being replaced by grazing-tolerant species. This has been shown by long-term studies (>10 years) on South African mesic grasslands that high grazing pressure and prolonged exclusion of fire results in the loss of most mesic grassland forbs with a community shift to more grazing-and shade-tolerant forbs (Fynn et al. 2005, Scott-Shaw and Morris 2015, Chamane SC unpublished data).

4.5 Conclusions

Findings of this study are consistent with other South African mesic grassland studies that showed the forb flora of these grasslands to be sensitive to grazing. Under sustained high grazing pressure many perennial forbs can be markedly reduced in abundance or eliminated and are replaced by grazing-resistant native and alien forbs and other species (Uys 2006, Scott-Shaw and Morris 2015, Chamane et al. 2016). The demography results revealed that future populations of the grazing-sensitive species (*Afroaster hispida*, *Agathisanthemum chlorophyllum* and *Gerbera ambigua*) may be under threat under HDG. Given that community-level indices offer little insight into the impact of grazing on forbs, a useful approach would be the identification of functional traits reflecting sensitivity and tolerance to grazing, including traits of their underground storage organs.

4.6 Acknowledgements

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CHAPTER 5: RESPONSE OF THREE PERENNIAL FORB SPECIES TO INTENSIVE DEFOLIATION AND INTERSPECIFIC COMPETITION IN MESIC GRASSLAND

5.1 Abstract

The importance of maintaining high biodiversity in natural grasslands under livestock production systems has been realised. However, little is known about how grazing and competition from neighbouring grasses impact on population dynamics of forbs, that contribute more to species richness than grasses. The aim of this study was to determine the response of three mesic grassland perennial forb species to intensive defoliation and interspecific competition from a neighbouring dominant grass, *Themeda triandra*, in a field experiment aimed at simulating intensive, frequent grazing. Two of the selected forb species are sensitive to defoliation (*Afroaster hispida* and *Gerbera ambigua)* and one is potentially resistant to defoliation (*Hypoxis hemerocallidea*). Only one species, *A. hispida*, showed an interaction response to intensive defoliation and competition. *A. hispida* had a high competitive response when undefoliated but when defoliated its competitive response was reduced. The benefit of reduced competition was observed for height after the 1st cut, where *A. hispida* recovered from defoliation under partial and no competition but not under full competition. *G. ambigua* was not affected by competition. *G. ambigua* and *H. hemerocallidea* were not affected by the interaction between defoliation and competition. These findings highlighted the importance of studying interactive effects of herbivory and interspecific competition on forb species responses.

Keywords: *grass-forb interaction; forb defoliation; competition; plant animal interactions*

5.2 Introduction

Commercial livestock production systems are not only important for sustainable livestock production but also for the maintenance of high biodiversity. However, historically research focused on grass composition and production because it comprises the bulk of livestock forage (Tainton 1999). The forb species (herbaceous dicotyledons and non-graminoid monocotyledons) which contribute most to plant diversity in natural grasslands (Morris 2004), but do not contribute significantly to the volume of forage consumed by livestock have consequently been largely ignored (O'Connor et al. 2010).

Plant population dynamics are known to be affected by herbivory and inter-species competition (Tilman 1988, Crawley and Ross 1990), but the interactive effects of herbivory and competition have not been well studied. In addition, the impacts of competition between species with varying growth forms are not clear. Selective herbivory is known to affect the competitive abilities of grasses by favouring certain species and reducing the competitive ability of others (Vesk and Westoby 2002). This occurs as a result of herbivores selecting for grazing sensitive species, which are usually palatable, and that leads to their replacement by the grazing tolerant species, which are usually unpalatable (Danckwerts and Stuart-Hill 1987, Hardy et al. 1999). This grazing induced shift in grass species led to the increaser-decreaser model, which has been commonly applied to the South African mesic grasses (Foran et al. 1978) but not to forbs because of a lack of suitable response data.

South African mesic grassland comprises a matrix of closed canopy, dense tufted perennial grass with scattered forbs. Commercial livestock farmers commonly use variations of the flexible rotational grazing system (Venter and Drewes 1969, Kirkman and Moore 1995). These grazing systems unlikely caused a major negative impact on forbs due to stocking at relatively low stocking densities, herewith referred to as LDG (O'Connor et al. 2010). At these low stocking densities, defoliation of forbs by trampling and grazing is low (Chamane et al. 2017). However, recently high-density, short-duration stocking (HDG) has been gaining popularity amongst farmers (Zietsman 2010, Phillips 2014) and under HDG, animals are stocked at higher stocking rates and densities than the other grazing systems (O'Connor et al. 2010), with resultant impacts on some forbs (Chamane et al. 2016).

Defoliation by consumption and trampling under HDG damages many forbs, leading to the potential demise of some species (Chamane et al. 2017). Palatable forb species with erect growth habits are more susceptible to consumption and species with soft fleshy leaves or stems are more susceptible to trampling impact (Chamane et al. 2017), while forb species with large storage organs have been shown to be resistant to defoliation (Del-Val and Crawley 2004). Competition from neighbouring grasses can enhance the negative influence of defoliation on forbs, as a result of competing for limited resources such as nutrients and light (Del-Val and Crawley 2004, Jensen and Löf 2017). This may be due to forbs occupying the same surface soil layers and being of similar height to grasses (Zaloumis 2013).

Grasses are known to be strong competitors for resources due to their growth form (Bond 2008, Cramer et al. 2010). Thus far, only a few studies have looked at how forbs respond to grass competition and they showed that under high grass competition forbs adjust their growth habit, for example an erect species would increase its height to stay at the same level as the grass for light (Zaloumis 2013). However, how intense defoliation under HDG alters grass/forb competitive relations, particularly the competitive response of South African mesic forbs is not known.

Plants living in close proximity to each other do not always compete for resources but they can also facilitate each other (Hunter and Aarssen 1988). Facilitation depends on the species identity or species strategy i.e. facilitative outcome of a species is a function of both low tolerance to environmental stress and strong competitive-response ability (Brooker and Callaghan 1998, Liancourt et al. 2005). Interactions among plants have been shown to shift from competition to facilitation along environmental gradients i.e. under stressful environmental conditions plants tend to facilitate each other rather than competing with each other (Holmgren et al. 1997, Brooker et al. 2007). In natural systems however, in the presence of other disturbances such as grazing, very few studies have assessed the interaction between competition and facilitation such as may occur, for example, between grasses and forbs (Callaway et al. 2002).

The aim of this study was to determine the response of three mesic grassland perennial forb species, *Afroaster hispida*; *Gerbera ambigua*; and *Hypoxis hemerocallidea*, to intensive defoliation (clipping used as a surrogate for grazing) and interspecific competition from a neighbouring dominant grass, *Themeda triandra* in a field experiment. The selection of forb species was based on their response to defoliation, availability of the species and variation in growth habit. *Afroaster hispida* and *Gerbera ambigua* are sensitive to intense defoliation (Scott-Shaw and Morris 2015, Chamane et al. 2017) and have an erect and prostrate growth habit respectively. *Hypoxis hemerocallidea* has a prostrate growth habit and is potentially more resistant to defoliation because it has a large swollen stem tuber compared to the other two species which have small to medium carrot like tubers. It was expected that (1) *A. hispida* and *G. ambigua* would have a higher competitive response than *H. hemerocallidea* when undefoliated, but (2) *H. hemerocallidea* would tolerate defoliation better than *A. hispida* and *G. ambigua*.

5.3 Materials and methods

5.3.1 The Study site

The experiment was conducted in a forb rich natural grassland (4 ha) on the campus of the University of KwaZulu-Natal, Pietermaritzburg (29º37'S 30º24'E), at an altitude of 675 m above sea level. The mean annual precipitation is 844 mm (Dent et al. 1987), falling mainly over the growing season (October to April). Summers are warm to hot with mean monthly maximum temperature of 27°C in February. Winters are cold with occasional frost and the mean monthly maximum temperature is 20.5°C in June. The soils are sandy clay loam textured and are classified as Westleigh and Mispah forms derived from the Ecca group shale of the Karoo sedimentary sequence (Turner 2000). The vegetation is classified as the Moist Midlands Mistbelt Grassland dominated by *Themeda Triandra* (Mucina et al. 2006). The area has not been grazed by livestock for at least the past 63 years and has been burned approximately biennially during this time.

5.3.2 Experimental design

The experiment followed a method proposed by Del-Val and Crawley (2004) which consists of various combinations of defoliation by clipping of the target or competitor plant or both plants, with the target species growing alone or under competition. The six treatment combinations were: two treatments with the target species growing alone, with one as (i) unclipped and the other (ii) clipped; four treatments had the target forb growing in competition with *T. triandra*, as (iii) control (both species unclipped), (iv) both species clipped, (v) only the target species clipped, and (vi) only the competitor clipped. The experimental design was a completely randomised 3 x 2 x 3 factorial with main effects of species (3 levels), defoliation (uncut, cut), and competition (alone, competition reduced through clipping of a competitor, full competition with competitor unclipped). There were ten replicate plants for each treatment combination. Treatments were randomly allocated to plants of each species. The selected plants were marked with wire and tags. The surrounding plants were cleared out by clipping all the aboveground material within 30 cm radius of the treatment plants. The area was regularly checked to ensure that the surrounding plants were cleared out for the duration of the experiment.

Intensive defoliation was applied by clipping an estimated 75% of the aboveground plant material of the target forbs and competitor, twice in the 2014/2015 growing season as a means of simulating grazing under high-density, short-duration grazing systems. The first clipping was done early in the growing season (December 2014) and the second clipping was done late in the growing season (February 2015). The second clipping was more intense i.e. the heights got lower due to the consistency of removing the same estimated amount from 1st clipping to the 2nd clipping. Measurements of plant height (mm) of the target plants were conducted in November 2014 before initial clipping, in February 2015, 60 days after the 1st clipping and again in April 2015, sixty days after the 2nd clipping.

At the end of the experiment in April 2015, all aboveground material of target plants was clipped and bagged separately, oven dried at 60°C for 48 h and weighed.

5.3.3 Statistical analysis

Analysis of variance followed by a least significant difference (LSD) was used to test for differences between treatment means, using IBM SPSS Version 24. Because initial plant height between species differed significantly (Figure 5.1), separate analyses were conducted for each species with aboveground drymass and height as response variables to test the main effects and interaction effects of defoliation and competition. A natural-log transformation for aboveground drymass and square-root transformation for height was applied to comply with analysis of variance assumptions, while the proportional response of treatment means was calculated from untransformed data.

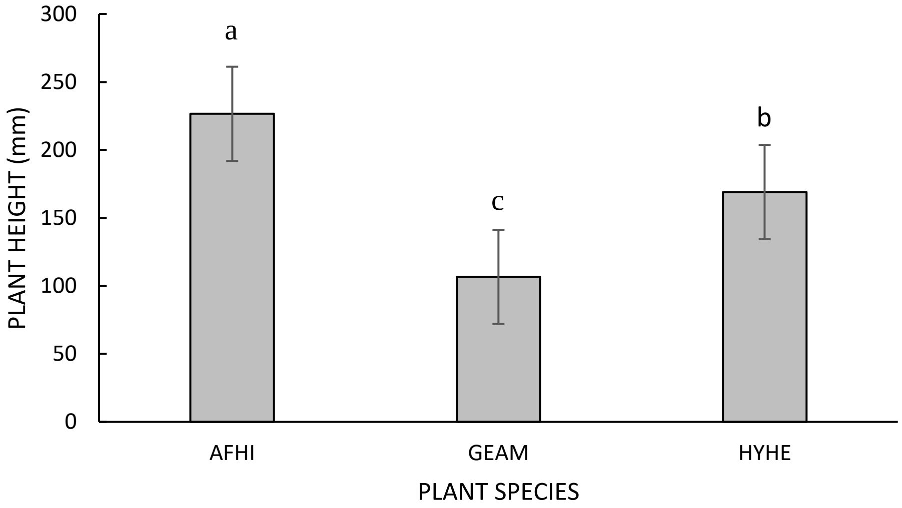

Figure 5.1: Plant height in mm (mean ± SE) of the selected individuals before the treatment was applied for *Afroaster hispida* (AFHI), *Gerbera ambigua* (GEAM) and *Hypoxis hemerocallidea* (HYHE), analysed using ANOVA, n = 60. Different letters above bars indicate differences in means ($p \leq 0.05$).

5.4 Results

Plant height did not differ within individual plants per species (*Afroaster hispida* $F_{(2,57)} = 0.236$, $p = 0.791$; *Gerbera ambigua* $F_{(2,57)} = 0.396$, $p = 0.675$ and *Hypoxis hemerocallidea* $F_{(2,57)} = 1.437$, $p = 0.246$) before the experiment. There was no interaction between defoliation and competition for all species expect for *A. hispida*'s height after the 1st cut (Table 5.1).

A. hispida had a high competitive response (aboveground mass and height was highest under full competition) when undefoliated but when defoliated its competitive response was reduced to 44% for aboveground drymass and 55% for plant height (Figure 5.2 and Table 5.2). The benefit of reduced competition was observed for height after the 1st cut, where *A. hispida* recovered from defoliation under partial and no competition conditions but not under full competition (Table 5.2). However, the aboveground mass and height after 2nd cut responses to defoliation did not depend on competition (Table 5.1). Defoliation reduced the aboveground mass of *A. hispida* by 31% and of the height after 2nd cut by 40% (Table 5.3).

G. ambigua showed a relatively low competitive response when undefoliated, aboveground drymass and height was highest where growing alone (Figure 5.2 and Table 5.2). Height after 1st cut of *G. ambigua* was not affected by defoliation or the interaction with competition (Table 5.1) indicating that *G. ambigua* is less sensitive to defoliation than *A. hispida*. However, similarly to *A. hispida*, defoliation reduced the aboveground mass of *G. ambigua* by 19% and of the height after 2nd cut by 27% irrespective of competition (Table 5.3).

H. hemerocallidea had a low competitive response when undefoliated, aboveground drymass was highest and it was the tallest when growing alone (Figure 5.2 and Table 5.2). The effect of defoliation did not depend on competition (Table 5.1). Defoliation reduced aboveground drymass by 33% and plant height after 2nd clipping by 35% irrespective of competition condition (Table 5.3). The presence of a competitor reduced aboveground drymass by 40% and plant height after 1st and 2nd clipping, by 20% and 30% respectively, irrespective of defoliation (Table 5.3).

Table 5.1: ANOVA results for treatment effects on natural log transformed aboveground drymass and square-root transformed height after 1st and 2nd regrowth of three *(Afroaster hispida*, *Gerbera ambigua* and *Hypoxis hemerocallidea)* forb species in a South African mesic grassland. Significant effects ($p \leq 0.05$) are in bold.

Treatment	df	Aboveground drymass (g)		Plant height (mm)			
				Cut 1		Cut 2	
		F	p	F	p	F	p
A. hispida							
Defoliation	1, 54	15.41	<**0.001**	12.18	**0.001**	30.59	<**0.001**
Competition	2, 54	0.52	0.595	1.30	0.281	2.32	0.108
Defoliation x competition	2, 54	2.61	0.083	6.22	**0.004**	2.28	0.112
G. ambigua							
Defoliation	1, 54	21.79	<**0.001**	12.99	0.072	13.45	**0.001**
Competition	2, 54	2.26	0.114	0.20	0.998	0.60	0.555
Defoliation x competition	2, 54	1.10	3.339	2.92	0.063	1.57	0.217
H. hemerocallidea							
Defoliation	1, 54	18.79	<**0.001**	1.31	0.256	21.17	<**0.001**
Competition	2, 54	16.55	<**0.001**	6.21	**0.004**	6.98	**0.002**
Defoliation x competition	2, 54	1.89	0.161	2.33	0.107	2.47	0.094

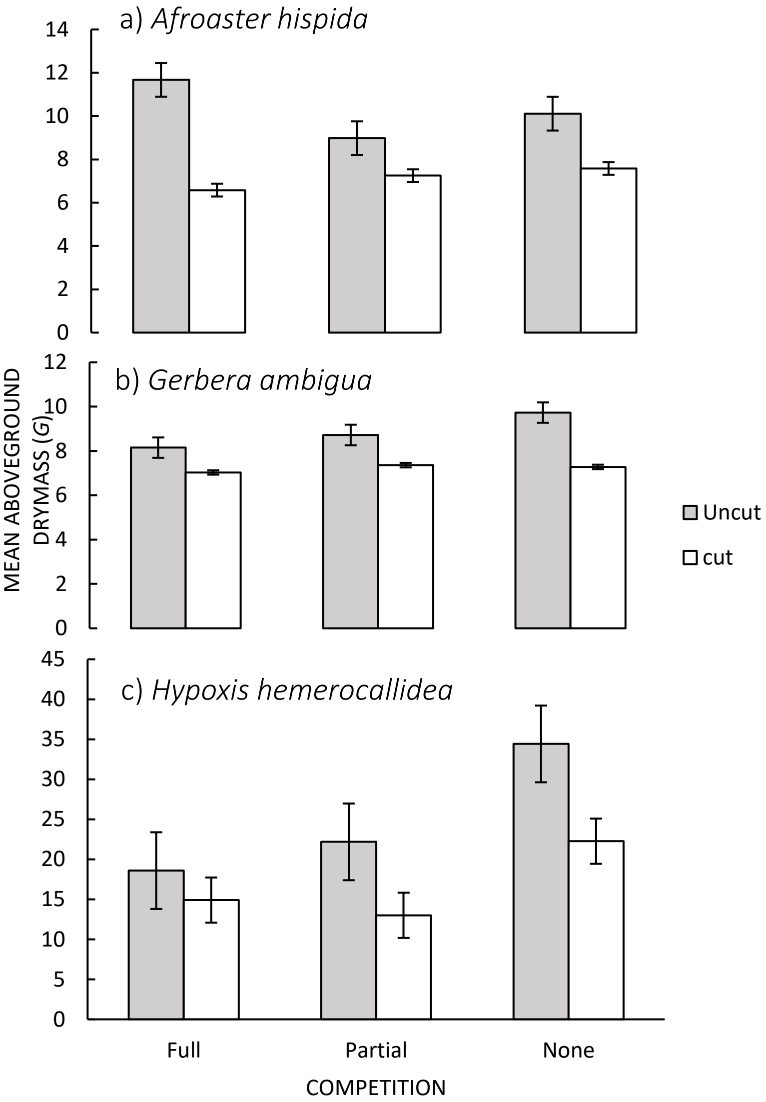

Figure 5.2: Aboveground dry mass (mean ± SE) of *Afroaster hispida*, *Gerbera ambigua* and *Hypoxis hemerocallidea* under simulated high-density, short-duration grazing (cut) growing alone (none) and in competition with *Themeda triandra.* In full competition the competitor was unclipped and under partial competition the competitor was clipped. (n = 10).

Table 5.2: Plant height in mm (mean ± SE) of *Afroaster hispida*, *Gerbera ambigua* and *Hypoxis hemerocallidea* under simulated high-density, short-duration grazing (cut) growing alone (none) and in competition with *Themeda triandra*. In full competition was where competitor was unclipped and partial competition was where competitor was clipped. Different letters indicate significant difference ($p \leq 0.05$) within competition type. Cut 1 was the measured regrowth after 1st clipping and cut 2 was regrowth after 2nd clipping ($n = 10$)

	Full competition		Partial competition		None	
	Uncut	Cut	Uncut	Cut	Uncut	Cut
Cut 1						
A. hispida	339.0 ± 27.95a	153.0 ± 23.61b	260.5 ± 19.39a	258.0 ± 27.76a	234.0 ± 38.93a	197.0 ± 24.54a
G. ambigua	170.0 ± 17.58	141.0 ± 11.71	163.5 ± 13.52	148.0 ± 14.70	186.0 ± 20.97	127.5 ± 12.14
H. hemerocallidea	217.0 ± 23.51	211.5 ± 11.16	231.5 ± 22.58	166.5 ± 22.14	276.0 ± 21.52	263.0 ± 23.11
Cut 2						
A. hispida	361.0 ± 49.39	176.0 ± 21.80	265.0 ± 14.66	197.0 ± 18.61	254.0 ± 33.81	161.0 ± 15.24
G. ambigua	160.0 ± 10.17	140.0 ± 34.43	154.0 ± 16.21	120.0 ± 14.20	169.0 ± 12.07	92.0 ± 10.17
H. hemerocallidea	212.5 ± 25.52	124.5 ± 12.37	212.5 ± 18.41	99.0 ± 6.86	253.0 ± 35.83	216.5 ± 26.68

Table 5.3: Plant height and aboveground drymass (means± SE) of *Afroaster hispida*, *Gerbera ambigua* and *Hypoxis hemerocallidea.* Only the significant main effects (defoliation and competition) are presented and ns = where there were no significant differences. Defoliation had two levels uncut and cut, n = 30. Competition had three levels, growing alone (none) and in competition with *Themeda triandra* where full competition was where competitor was unclipped and partial competition was where competitor was clipped, n = 20. Different letters indicate significant difference ($p \leq 0.05$) within competition.

Variable	Defoliation		Competition		
	Uncut	cut	Full	Partial	None
Afroaster hispida					
Drymass (g)	10.3 ± 0.71	7.1 ± 0.71	ns	ns	ns
Plant height after 2nd clipping (mm)	293.7 ± 16.42	178.0 ± 16.42	ns	ns	ns
Gerbera ambigua					
Drymass (g)	8.9 ± 0.26	7.2 ± 0.26	ns	ns	ns
Plant height after 2nd clipping (mm)	161 ± 10.55	117.7 ± 10.55	ns	ns	ns
Hypoxis hemerocallidea					
Drymass (g)	25.1 ± 1.52	16.7 ± 1.52	16.7 ± 1.86b	17.6 ± 1.86b	28.3 ± 1.86a
Plant height after 1st clipping (mm)	ns	ns	214.3 ± 14.93b	199.0 ± 14.93b	269.5 ± 14.93a
Plant height after 2nd clipping (mm)	226.0 ± 13.30	146.7 ± 13.30	168.5 ± 16.30b	155.8 ± 16.30b	234.8 ± 16.30a

5.4 Discussion

5.4.1Responses of three forb species to defoliation and competition

The ability of plants to recover from defoliation can be affected by competition (Vesk and Westoby 2002, Del-Val and Crawley 2005). This was only the case for *Afroaster hispida* where plant height after the 1st cut was reduced under full competition. For *Gerbera ambigua* and *Hypoxis hemerocallidea*, recovery from defoliation was not affected by competition for all variables.

Afroaster hispida benefited from reduced competition i.e. partial and no competition when defoliated, possibly because of it erect growth habit (Chamane et al. 2017), which is similar to *T. triandra* (the competitor) as a result they may have competed for light. Since *T. triandra* had more leaves with greater surface area than *A. hispida* that may have made it a better competitor (Briske and Richards 1995). Thus when *T. triandra* was also defoliated, that may have reduced its competitive ability on *A. hispida.* The reduction of competition by defoliating neighbouring plants had been shown to reduce the influence of defoliation on target plants (Morris and Tainton 1993, Wardle and Barker 1997).

G. ambigua was not affected by the interaction between defoliation and competition. The possible reason for that might be because it did not need to compete with the dominant grass for light due to its prostrate growth habit with wide leaves compared to the dominant grass, which had an erect growth habit and narrow leaves (Diaz et al. 2007, Chamane et al. 2016).

Hypoxis hemerocallidea is a monocot, while the other two forb species are dicots. *H. hemerocallidea* has a basal meristem, similarly to the grasses, which is an adaptation to grazing because the meristematic regions are more protected from defoliation at the base of the plant (Hawkes and Sullivan 2001). *Afroaster hispida* and *G. ambigua* have an apical meristem habit which is more exposed to defoliation. Hence, *Hypoxis hemerocallidea* was expected not to be affected by defoliation. *Hypoxis hemerocallidea* was, however, only resistant to defoliation for plant height after the 1st cut irrespective of competition condition. This indicates that although *Hypoxis hemerocallidea,* is adapted to defoliation, high grazing pressure may negatively affect it.

5.4.2 Management implications

A. hispida had a high competitive response when undefoliated (Figure 5.2 and Table 5.2), indicating that under LDG systems where it may either be undefoliated or leniently defoliated it would still persist irrespective of the competition condition. It appears to have the ability to adjust it growth habit in the presence of a competitor (Zaloumis 2013). However, under HDG where it is likely to be defoliated either by grazing or trampling (Chamane et al. 2017), its competitive response can be reduced (Figure 5.2 and Table 5.2). This can potentially have a negative impact where it is growing in the presence of an undefoliated competitor i.e. full competition.

The effect of the 2nd cut was more pronounced than the 1st cut on the height of *G. ambigua* and *H. hemerocallidea* irrespective of competition conditions (Table 5.1 and Table 5.3). This indicates that the effect of HDG on these forbs may be more detrimental when applied twice in the growing season. The intense repeated defoliation potentially leads to the depletion of energy reserves and they do not get a chance to be replenished. That can reduce the plant vigour and over time the storage organ of the plant and may eventually lead to the demise of the plant. Alternatively, other factors may have had an overriding effect for example the timing of defoliation or the physiological stage of the plant species during defoliation (Maschinski and Whitham 1989, Rosenthal and Kotanen 1994).

5.5 Conclusions

The importance of assessing herbivory on the complex plant-plant interactions were highlighted by this study. Only *A. hispida* showed an interaction effect of defoliation and competition. *A. hispida* had a high competitive response when undefoliated and defoliation reduced its competitive ability. However, under no competition or reduced competition, *A. hispida* was able to recover from defoliation. *Gerbera ambigua* was not affected by competition and *H. hemerocallidea* had a low competitive response irrespective of defoliation.

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CHAPTER 6: GENERAL DISCUSSION AND CONCLUSIONS

6.1 Introduction

South African mesic grasslands on nutrient poor soils are rich in plant species and diversity (Cowling et al. 1991). They contain a matrix of perennial grasses with numerous scattered species of forbs (herbaceous dicotyledon and non-graminoid monocotyledon) with underground storage organs. Fire plays a critical role in these grasslands in maintaining them as grasslands and stimulating resprouting of the forbs from their underground storage organs (Uys et al. 2004). The dominant land use in these natural grasslands is livestock production, particularly cattle (Palmer and Ainslie 2005). Grazing management systems commonly used in mesic South African grasslands include fire as a management tool (Kirkman and Moore 1995). Over the past decades, an extreme rotational grazing system i.e. high-density, short-duration stocking (HDG) (Savory and Butterfield 2016), has been gaining popularity in the mesic grasslands. It advocates the replacement of fire with high density stocking under higher stocking rates compared to conventional rotational grazing systems at lower density stocking (LDG) (O'Connor et al. 2010). There is no empirical evidence of the impact of HDG on natural resources on South African mesic grasslands. The aim of this study was to determine the effect of HDG on vegetation dynamics and plant species composition with the key focus on forbs as they constitute most of the plant diversity in South African grasslands.

6.2 Summary of contributions

6.2.1 Can high density stocking replace fire in mesic grasslands?

Findings from this study show that high density stocking cannot replace fire in South African mesic grasslands. HDG contends that the exclusion of fire results in high litter accumulation which increases water availability (Savory and Butterfield 2016). In mesic grasslands however, water or moisture is not limited since they receive relatively high stable rainfall. This study has shown that the replacement of fire with HDG resulted in the accumulation of a thick and heavy litter layer that reduced live vegetation cover over the long- (Chapter 3) and short-term period (Chapter 4).

Findings from this study have shown that replacing fire with grazing potentially results in shifts in the abundance of grass species, with the palatable grasses being less abundant under HDG compared to LDG and a high forb species turnover between HDG and LDG, indicating that fire dependent species were replaced with fire independent species under HDG (Chapter

3). These findings are inline with other South African mesic grassland studies that have shown that excluding fire results in a decline in abundance of the palatable grasses (Everson et al. 1985, Trollope 1999, Everson et al. 2009, Fynn et al. 2011) and shifts in forb species composition (Titshall et al. 2000, Fynn et al. 2004, Uys et al. 2004, Fynn et al. 2005).

The species shifts observed in this study were over a long-term period of 19 years (Chapter 3) and the forb species that were replaced are likely lost forever as the resprouting forb species have been shown to persist for up to 8 – 10 years without fire after which they disappear permanently (Fynn et al. 2004, Uys et al. 2004). Where fire was excluded under both HDG and LDG, a low forb species turnover was observed indicating that under both systems fire dependent species were probably lost and had been replaced by the fire independent species and the low species shifts observed were probably due to the differences in stocking densities between systems (Chapter 3). These findings indicate that fire has an overriding effect over grazing and that it is important in maintaining the structure and functioning on South African mesic grasslands and cannot be replaced with grazing.

6.2.2 Can mesic forbs withstand HDG?

Findings from this study have shown that over long- (Chapter 3) and short-term periods (Chapter 4 and Chapter 5) HDG negatively affected perennial mesic forbs. Although findings from this study (Chapter 3) and other South African mesic grassland have shown that high grazing pressure results in shifts in forb species composition (Uys 2006, Scott-Shaw and Morris 2015) but there was no change on diversity indices (Chapter 3 and Chapter 4). A similar trend has been reported by a meta-analysis study that showed that in mesic grasslands, grazing induces strong shifts in species composition with little or no change in species richness and diversity (Herrero-Jáuregui and Oesterheld 2018). This is possibly because mesic grasslands have more species with adaptive traits, so that when grazing sensitive species are lost grazing tolerant species replace them and diversity indices fail to pick up these shifts in species composition. This was supported by findings in this study that showed that HDG promoted prostrate growth habits over erect growth habits (Chapter 3). This study has highlighted the need and the importance of identifying more functional traits, other than growth or life form, that are sensitive and resistant to grazing impacts (Diaz et al. 2007) rather than using diversity indices in order to understand the grazing impacts on plant species composition in mesic grasslands.

The results obtained in this study over the short term period (Chapter 4 and Chapter 5) are important in terms of improving our understanding on the effect of HDG on mesic forbs.

In particular, how HDG affects the demography of grazing sensitive forbs (Chapter 4); how HDG through consumption and trampling affects forbs (Chapter 4) and how intense defoliation and interspecific competition affects forbs (Chapter 5). Understanding the above factors can give us an insight as to what drives species compositional changes under HDG.

The demography component of this study revealed that HDG increased the mortality of the grazing sensitive species which was measured as complete above-ground biomass loss, but below-ground biomass may have still been alive (Chapter 4). This implies that should such conditions continue even the below-ground biomass would be lost resulting in eventual complete mortality.

The uncommon species were either severely damaged or undamaged by the direct impact of HDG through consumption and trampling (Chapter 4). The high variation in the response of uncommon species may be due to different plant species functional traits. For example tall statured plants which are palatable may be susceptible to grazing while forbs with fleshy stems and leaves may be more susceptible to trampling. This implies that the rare species with traits that are susceptible to grazing or trampling impact would be lost at a faster rate under HDG compared to conventional rotational grazing systems at conservative stocking rates.

This study has also shown that it is the repeated intense defoliation that potentially has more chronic consequences for the perennial mesic forbs compared to when defoliated once (Chapter 5). Although mesic forbs have large underground storage organs, the repeated intense defoliation as may be experienced under HDG, may force the forbs to draw from their energy reserves to try and recover after each defoliation event. Due to the intense defoliation being repeated, the plant may not get sufficient time to replenish its energy reserve and that can reduce the plant vigour and over time it might reduce the storage organ of the plant and eventually leading to the demise of the plant. Hence, it is the repeated impact of HDG that is detrimental to mesic forbs.

6.3 Management recommendations for South African mesic grasslands

In South African mesic grasslands, more frequent fires increase plant diversity, promotes resprouting of mesic forbs with underground storage organs, reduces phytomass and litter mass, opens up space for the forbs to flourish and increases tiller production of the palatable grasses (Uys et al. 2004, Chapter 3). Although more frequent burns are recommended for the mesic grasslands, annual burning in the presence of grazing is not advised because it reduces the forage production potential for livestock (Barnes 1992). Grazing alone either under HDG or LDG changes the forb species composition and reduces the abundance of palatable grasses and thus cannot maintain the structure and functioning of South African mesic grasslands (Chapter 3). High stocking rate and stocking densities irrespective of grazing management system reduces the cover of palatable grasses and causes a detrimental impact on mesic forbs and increases the cover of ruderal annual or alien forb species (Chapter 3 and Chapter 4). Therefore, in order to sustain livestock production and maintain biodiversity in South African mesic grasslands, frequent fires (2 - 4 years) and moderate stocking rates and stocking densities are recommended.

6.4 Future possibilities

This study has improved our understanding on the effect of HDG over the short- and long-term on vegetation dynamics and forb species composition. Further knowledge gaps not yet addressed include determining the time (greater than 3 years but less 10 years) at which the forb species shifts start to occur under HDG; for both short- and long-term comparisons of HDG, determining if the underground storage organs are dormant or if they have been removed when the above-ground biomass is gone completely. Furthermore, to determine the diversity of below ground biomass of forbs between HDG and conventional rotational grazing systems. Identify forb functional traits that are sensitive and resistant to grazing which would take into account the presence and nature of underground storage organs. Identification of these traits will better facilitate the mainstreaming of plant diversity into livestock production systems.

6.5 Final comments and summary conclusions

This study has shown that HDG may potentially have negative impact on the natural resources of a South African mesic grassland for both sustainable production of livestock and biodiversity conservation. The absence of burning coupled with high grazing and trampling impact under HDG resulted in a decline of the palatable grass species and a shift in forb species composition with the grazing sensitive, fire dependent species being replaced by the grazing tolerant, fire independent species which included ruderal, annual and alien invasive species.

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