EXPLORING ECOSYSTEM FUNCTIONING, SERVICE PROVISION AND MANAGEMENT OPTIONS ON GRAZED SEMI-ARID RANGELANDS UNDER CLIMATE CHANGE

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[redacted]

A RESEARCH THESIS
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Abstract

Global environmental change is increasingly recognised as a concern particularly in dry rangelands where livelihoods rely heavily on ecosystem services from climate sensitive agriculture. Current models predict rising temperatures and decreasing precipitation with high variability, and increasing frequencies of droughts in these ecosystems. For African rangelands, livestock numbers are also expected to increase in response to increasing human population. These changes, in combination, are expected to impact negatively on ecosystem function and service provision with devastating effects particularly in Africa due to the high rural populations that have a low adaptive capacity. Thus it is critical to advance ecological understanding of these systems' response and resistance to the effects of drought and grazing.

Motivated by both the current condition and predicted changes in local rangelands, the overall aim of this study was to explore ecosystem function and service provision in grazed semi-arid rangelands and ultimately suggest viable management options and adaptation strategies. Four questions were asked in this regard; 1) Do existing drought and grazing literature adequately address predicted future climate change scenarios particularly in the context of southern African rangelands? 2) How can the knowledge gaps in drought and grazing (combined) studies be overcome in these ecosystems? 3) How does ranch-scale grazing management influence herbaceous and woody vegetation dynamics? and 4) How does herbivore impact and recovery periods influence rangeland dynamics in climatically variable semi-arid ecosystems?

In order to answer the above questions, this study carried out a critical review of drought and grazing literature to evaluate the relevance of conventional grazing research in the wake of global environmental change. The study also established a large-scale experiment that combines precipitation manipulations with cattle grazing and possible management options in the rangelands of Limpopo Province – South Africa to complement plot-scale clipping and ranch-scale grazing case studies conducted in semi-arid rangelands of southwestern Botswana. The review revealed that grazing-related research is well documented in Africa, although it lacks certain levels of realism in terms of scales (temporal and spatial), study designs (e.g. common garden *vs* in situ manipulations) and the nature of treatments (i.e. clipping *vs* grazing), whereas relevant drought (and / or grazing) research is lacking. Furthermore, from the review, it was demonstrated that dry rangelands are complex ecosystems that require multifactorial standardized experimental approaches to study individual and interactive effects of several ecosystem drivers simultaneously.

The study also established a novel experimental approach that combines real grazing with extreme drought (according to the standardized precipitation index specific to the area) and found that optimal vegetation performance in previously undegraded veld, should be obtained by growing-season resting for durations not exceeding one season, even under extreme drought conditions, to avoid an accumulation of standing dead material that inhibits new growth. From ranch-scale case studies of grazing management, the results demonstrated that rangeland health (as measured by cover of palatable perennial grasses) in degraded areas (i.e. areas with increased woody vegetation cover and less herbage) may not be achieved by destocking alone – as is usually common practice, but through adaptive management at appropriate scales that involve uniform grazing and adequate season-long grazing – an approach that may be achieved on rotationally grazed (RG) rather than continuously grazed (CG) systems. Furthermore, the study found through clipping experiments that while broad-leaved palatable perennial grasses such as *Brachiaria nigropedata* are able to overcompensate under clipping, their productivity decreases with increasing previous season clipping frequency – an example of lagged effects of grazing history, whereas less palatable needle-leaved species such *Stipagrostis uniplumis* are less resistant to grazing. In addition, the importance of mechanistic components of herbivory (defoliation, trampling and nutrient deposition) in clipping experiments were highlighted where the interaction of clipping, dung and trampling increased grass cover, contrary to the neutral response from their individual effects.

In conclusion, this PhD has advanced scientific knowledge on grazed ecosystems and how they may be impacted by predicted global environmental changes. The study also has important implications for theory, management and policy particularly with respect to drought mitigation and adaptation strategies. Suggestions are made for grazing management as well as feeding strategies during and after drought years to help the veld to recover. Thus, rangelands with a long evolutionary history of grazing, such as those in southern African savannas, are expected to show some convergent responses to grazing and extreme drought conditions, the strength and direction of which will be determined by the underlying grazing management. The findings of this thesis may be applied to alleviate problems of grazing-related degradation in semi-arid rangelands of Limpopo and elsewhere, and also to develop adaptation strategies for predicted future global change challenges.

DECLARATION

I declare that the thesis hereby submitted to the University of Limpopo, for the degree of Doctor of Philosophy in Agriculture (Animal Production – Rangeland Ecology) has not previously been submitted by me for a degree at this or any other university; that it is my work in design and in execution, and that all material contained herein has been duly acknowledged.

Edwin Mudongo (Mr)

Date

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Acknowledgements

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List of Acronyms

AGB	Aboveground Biomass
ANOVA	Analysis of Variance
ANPP	Aboveground Net Primary Production
C1	Clipped (twice) every year
C2	Clipped (twice) every alternate year
CDE	Coordinated Distributed Experiments
CEC	Cation Exchange Capacity
CF	Clipped five times every year
CG	Continuous Grazing
COF	Clipped once only
DAHP	Department of Animal Health and Production
EF	Ecosystem Function
ES	Ecosystem Services
ESR	Early Season Rest
FSR	Full Season Rest
GO	Grazing Offtake
GRA	Grazed plot
IDE	International Drought Experiment
IPCC	Intergovernmental Panel on Climate Change
LSR	Late Season Rest
LSU	Large Stock Unit
LTE	Long-term Exclosure

MAP	Mean Annual Precipitation
MEA	Millennium Ecosystem Assessment
NR	No Rest
ORI	Okavango Research Institute
PAR	Photosynthetic Active Radiation
RG	Rotational Grazing
SPI	Standardized Precipitation Index
STE	Short-term Exclosure

List of publications

Publications in the thesis

Mudongo, E.I., Fynn, R.W. and Bonyongo, M.C., 2016a. Role of herbivore impact and subsequent timing and extent of recovery periods in rangelands. *Rangeland Ecology & Management* 69: 327 – 333.

Mudongo, E.I., Fusi, T., Fynn, R.W.S. and Bonyongo, M.C., 2016b. The role of cattle grazing management on perennial grass and woody vegetation cover in semiarid rangelands: Insights from two case studies in the Botswana Kalahari. *Rangelands* 38: 285 – 291.

Edwin I. Mudongo, Jan C. Ruppert, Kingsley K. Ayisi. Evaluating relevance of conventional grazing research under global change - A review of drought and grazing studies: **Submitted** - *African Journal of Range and Forage Science*

Mudongo, E.I., Ruppert, J.C. and Linstaedter, A. Adding realism and management options to global change experiments: the DroughtAct approach. ***In preparation***

Other publications

Canak, K., Ruppert J.C., Linstaedter, A., **Mudongo, E.I**., Lema, N. and Schmidtlein, S. Estimating plot-level biomass of herbaceous species via allometric models – recommendations for optimal measurement strategies. ***In preparation***

Mudongo, E.I. and Keitsile O.A. The influence of rainfall variability and land use on springbok (*Antidorcas marsupialis*) population dynamics in southwestern Botswana: **Submitted** - *Scientifica*

Pfeiffer, M., Langan, L., Linstaedter, A., … **Mudongo, E.I**., … Grazing and aridity reduce perennial grass abundance in semi-arid rangelands – insights from a trait-based dynamic vegetation model.: **Submitted** - *New Phytologist*

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Mudongo, E.I., Ruppert, J.C., Frank, A., Ayisi, K.K., Ngambi, J. and Linstaedter, A. 2016. Should we rest the veld during drought? 3rd National Conference on Global Change. Durban, South Africa. *http://globalchange2016.ukzn.ac.za/Homepage.aspx*

Mudongo, E.I., Ruppert, J.C., A., Ayisi, K.K., Ngambi, J. and Linstaedter, A. 2017. Exploring grazed ecosystems functioning and management options under extreme drought conditions in Limpopo, South Africa. The 4th Global Science

Conference on Climate Smart Agriculture. Johannesburg, South Africa. http://csa2017.nepad.org/en

CHAPTER 1: General Introduction

1.1 Dry rangelands

Drylands cover >40% of the earth's land surface and are home to approximately one third of the human population (MEA, 2005, Reynolds et al., 2007). These ecosystems occur across all continents and are predominant in Africa (and Australia, Fig. 1.1), e.g. the form of savanna and grassland biomes of Sub-Saharan Africa in general and southern Africa in particular (Havstad et al., 2008). Drylands comprise regions with hyper arid , arid , semi-arid and dry-sub humid climates (Table 1.1) (Mortimore et al., 2009). Rangelands are the predominant landuse type and account for 65% of the world's dryland area, 54% of which are located in semi-arid climates (Table 1.1). These extensive natural landscapes are characterized by low and highly variable productivity from low-fertility soils that are unsuited for crop cultivation, and vegetation that is dominated by native grasses, forbs and shrubs (Havstad et al., 2008).

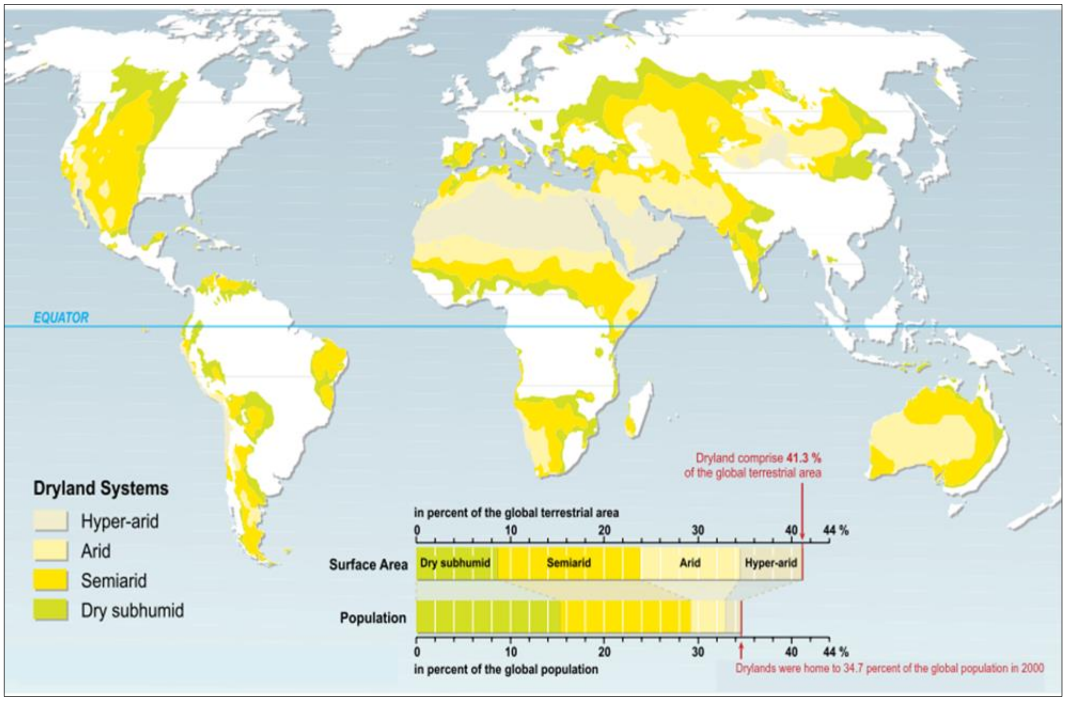

Figure 1.1: Distribution of the world's drylands by aridity index. Adopted from MEA (2005a).

Table 1.1: Proportion of land area, population and landuse by different dryland systems. Adopted from Mortimore (2009).

Type	Aridity index	% of global area	% of global population	% Rangeland	% Cultivated	% Other
Hyper-arid	< 0.05	6.6	1.7	97.0	0.6	3.0
Arid	0.05 - 0.2	10.6	4.1	87.0	7.0	6.0
Semi-arid	0.2 - 0.5	15.2	14.4	**54.0**	35.0	10.0
Dry sub-humid	0.5 - 0.65	8.7	15.3	34.0	47.0	20.0
Total		41.3	35.5	**65.0**	25.0	10.0

Rangelands provide habitat for both domestic and wild herbivores, but today the most dominant landuse in these ecosystems is livestock husbandry as it is the most important source of income that provides livelihood security, particularly in rural areas (Martin et al., 2016). The highly variable climatic conditions, where rainfall is low and stochastic (IPCC, 2014), the scarcity of soil moisture and infertility of the soils (Mortimore et al., 2009, Maestre et al., 2012), makes dryland rangelands only favourable for pastoralism (Martin et al., 2016). Thus, forage production from natural rain-fed rangelands is an important ecosystem service that supports livelihoods in these ecosystems (Gillson and Hoffman, 2007).

Semi-arid rangelands are the most vulnerable to loss of ecosystem services due to the relatively high population in relation to their productive capacity (MEA, 2005). Approximately 10 to 20% of the world's rangelands have been judged as degraded (Reynolds et al., 2007), i.e. lacking the capacity to yield provisioning, regulating, and supporting ecosystem services (DeFries et al., 2004, MEA, 2005). Some of the causes of degradation in rangelands are associated with livestock grazing at rates that exceed carrying capacities of the ecosystem, and climate change, which affects rates of rainfall patterns (amount and distribution) and evapotranspiration (MEA, 2005). Therefore, the challenge faced by rangeland ecologists and managers globally is to find and maintain livestock numbers that do not compromise the functionality and structure of these vulnerable ecosystems (Bagchi et al., 2012), in order to achieve "win-win" or "small loss-big gain" relationships (Fig. 1.2). In this context, it is important to understand the mechanistic functioning of rangeland ecosystems as well as the prime external drivers that influence ecosystem processes.

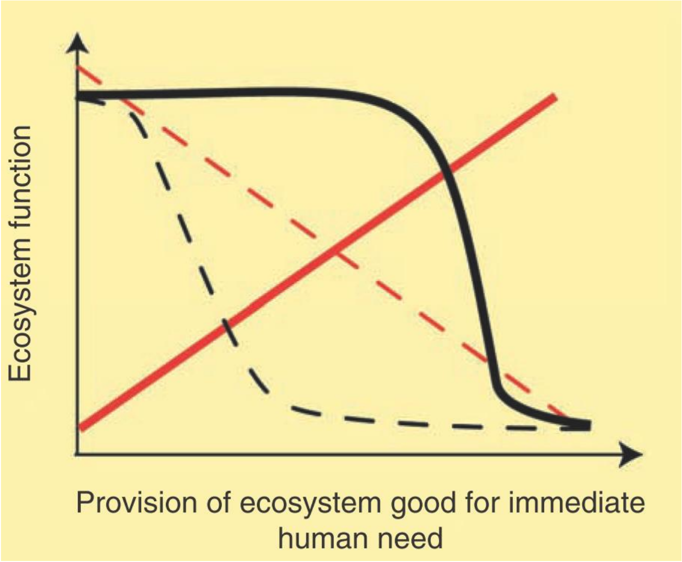

Figure 1.2: Examples of possible relationships between ecosystem function and ecosystem service provision for human needs such as livestock forage availability. A “win-win” situation (red line) is achieved when ecosystem function increases with service provision, while a “small loss-big gain” (solid black line) relationship is achieved when small reduction in ecosystem function yields large gains in ecosystem services. Degradation relationships include the “win-loss” (dotted red line) where ecosystem function decreases with increasing service provision and “big loss-small gain” where major decreases of ecosystem function yields very small services. Reproduced from DeFries et al (2004).

1.2 Primary drivers of ecosystem function (EF) in rangelands

The functioning of semi-arid rangeland ecosystems is driven by a number of factors. Climate, fire and grazing are key factors driving EF through their direct influence on vegetation dynamics in drylands (Koerner and Collins, 2014, Ruppert, 2014). However, fire and grazing influences are constrained by the underlying climate, particularly precipitation (Milchunas and Lauenroth, 1993, Collins et al., 2012). Edaphic factors (physical and chemical) also play an important role in influencing response patterns of grazed ecosystems (Archer and Smith, 1972, Rezaei and Gilkes, 2005) However, the effects of fire are beyond the scope of the study.

1.2.1 Precipitation

Climatic factors, particularly precipitation and hence soil moisture, has been identified as a primary limiting factor for forage provision in semi-arid rangelands (Coe et al., 1976, Sala et al., 1988, Ruppert et al., 2012, Linstädter and Baumann, 2013). Forage provision is mostly assessed as aboveground net primary production (ANPP), i.e. the total of assimilated plant material less respirational losses, or surrogates thereof (e.g. aboveground biomass at peak standing crop). The amount, distribution and variability of annual precipitation has strong effects on dry ecosystems' productivity and carrying capacity (Coe et al., 1976, Sala et al., 1988) and strongly affects plant community composition (Scholes and Walker, 2004).

Plant biomass increases with mean annual precipitation (Sala et al., 1988, Yahdjian and Sala, 2006). But, it is a growing season's precipitation that has more marked effects on primary production than annual precipitation (Nippert et al., 2006, La Pierre et al., 2011, Robinson et al., 2013). For arid and semi-arid rangelands, precipitation also has a positive linear relationship with species richness and turnover (Cleland et al., 2013). While current season's precipitation has direct influences on plant growth rates, also previous season rainfall influences ANPP through 'legacy effects' (Reichmann et al 2013), e.g. mediated via storage tissues or seed production in perennial or annual species, respectively. Thus, precipitation forms an integral part of grazing research in semi-arid rangelands.

1.2.2 Grazing

Grazing is the most extensive form of landuse on earth, with estimates of the area occupied by managed rangelands ranging between 25 and 50% of the global land surface

(Asner et al., 2004) (Havstad et al., 2008). For arid and semi-arid rangelands with marginal bioclimatic conditions, grazing may lead to land degradation (Reynolds et al., 2007). Degradation, the net loss of capacity to yield provisioning, regulating, and supporting ecosystem services (MEA, 2005a), is commonly related to phenomena such as desertification and woody encroachment (Asner et al., 2004). However, the level of degradation often depends on the intensity of grazing and resilience and resistance of the ecosystem (Hoover et al., 2014).

Moreover, the response of different dryland ecosystems to grazing is often related to their evolutionary history of grazing (Milchunas et al., 1988). The basis if this concept comes from the idea that vegetation in regions that have been subjected to large herbivore grazing for prolonged evolutionary times such as African savannas, is well adapted to grazing (i.e. shows certain levels of grazing tolerance). Actually, moderate levels of grazing in these systems may even lead to overcompensation – a condition where regrowth after defoliation exceeds tissue loss. In this regard, lack of grazing may even lead to degradation in these areas although the opposite may be true in some cases (Ruppert, 2014).

Indicators of desertification in grazing lands vary from reductions in primary production (Prince et al., 1998) to changes in plant community composition (Schlesinger et al., 1990) and increases of bare and eroded soil surfaces (Okin et al., 2001). Increase in grazing intensity reduces standing biomass and cover, hence exposing the soil to risks of erosion by wind or run-off and nutrient loss by volatilization (O'Connor et al., 2001, Hoffmann et al., 2008, Schönbach et al., 2011). Nevertheless, grazing effects reported across different rangeland environments have been variable and the variability has been linked to various aspects of grazing relating to scales and magnitude. Thus, more empirical and theoretical knowledge is needed to understand the dynamics of semi-arid rangelands' response to grazing in the face of climate change.

1.2.3 Edaphic factors

Soil chemical and physical properties play important roles in supporting plant growth. Physical properties such as particle size, bulk density and associated water holding capacity determine infiltration, retention and supply of water as well as nutrient cycling, aeration and plant root penetration (Rezaei and Gilkes, 2005). Ultimately, these properties determine how much of the received precipitation is available for uptake by plants (Archer and Smith, 1972), making them important for semi-arid rangelands where plant available water is low and erratic, be it due to low precipitation or due to high evaporation. Like physical properties, soil chemical properties, particularly macro-nutrients (carbon, nitrogen and phosphorus), are also crucial in dryland rangelands as they may limit production (Delgado-Baquerizo et al., 2013) apart or beyond water limitation.

However, soil properties are not static but also affected by changing climatic conditions, grazing management regimes as well as vegetation itself. A global assessment of available nutrients in dryland soils showed reduction in C and N, and increases in inorganic P with increasing aridity (Delgado-Baquerizo et al., 2013). Similarly, continuous grazing resulted in considerable loss of C, N and biological properties in the soil due to reduced vegetation cover and subsequent soil erosion, whereas conditions improved with increasing time of grazing exclusion in semi-arid rangelands of China (Yong-Zhong et al., 2005, Jing et al., 2014). Thus, it is important to understand the dynamics of both physical and chemical soil properties in rangelands as they have close association with climate and grazing management.

1.3 Current and projected global change in dry rangelands

In the present day, dry rangelands are faced with an increase in global human population with high reliance on livestock keeping as a major livelihood activity (MEA, 2005a). Livestock production in these systems depends heavily on provision of ecosystem services from natural rain-fed vegetation (Martin et al., 2014, Martin et al., 2016). Many of these ecosystems are characterized by uncertainty as a result of low and erratic rainfall, including droughts, that limits primary production (Reynolds et al., 2007, Zhao and Running, 2010, Ruppert et al., 2012) on already relatively low fertility soils (Maestre et al., 2012, IPCC, 2014). Besides, climate change models predict decreasing predictability and an increase in inter and intra-annual variability in precipitation regimes, as well as increasing frequency of more extreme events that include multiyear droughts with potential to impact significantly on provision of ecosystem services globally (Knapp et al., 2008, Cherwin and Knapp, 2012, IPCC, 2014). Generally, semi-arid drylands – particularly those in Africa – are expected to suffer from increases in aridity by the end of the 21st century, due to increased surface temperatures (up to 2°C) and reduced precipitation (up to 10%, Fig. 1.3).

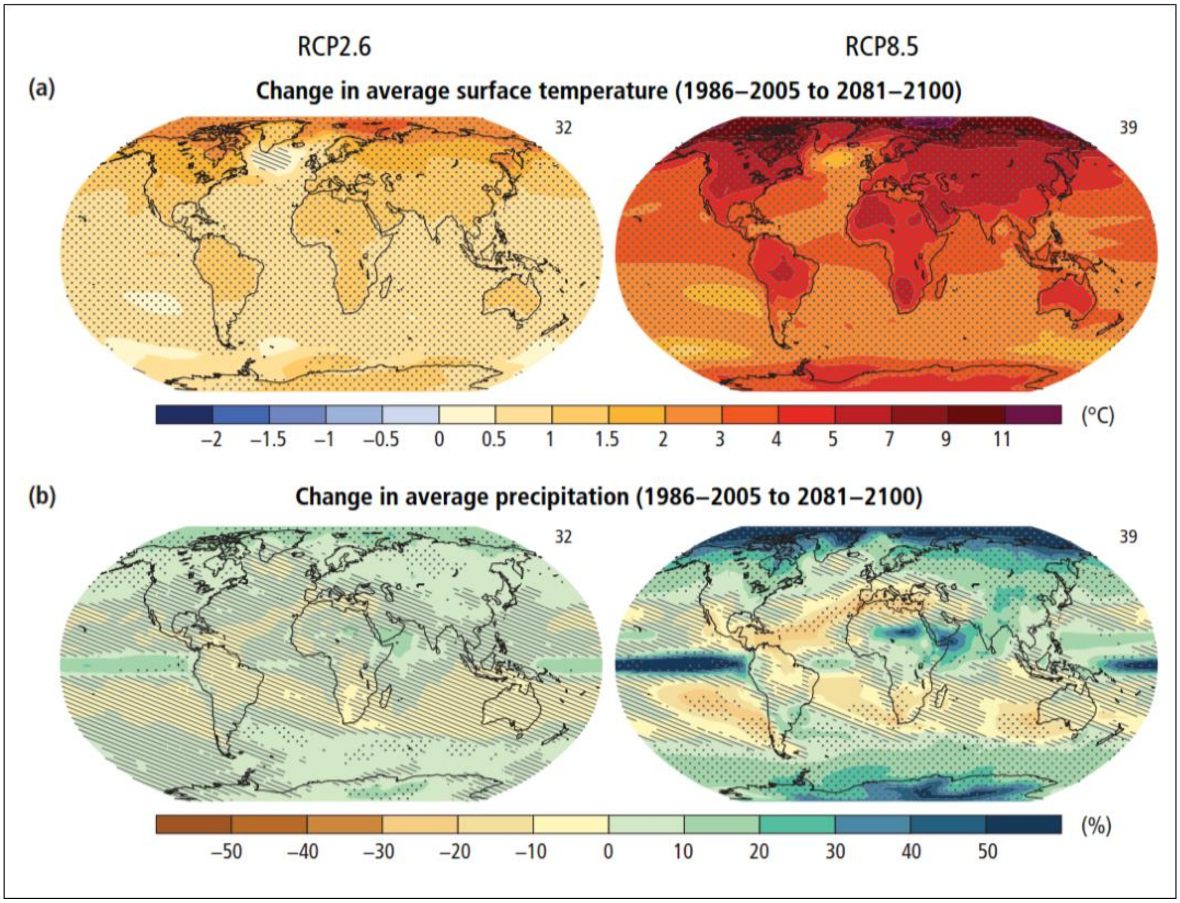

Figure 1.3: Global projections of future climatic scenarios for temperature (**a**) and precipitation change (**b**) based on 1986 – 2005 baseline period. Adopted from IPCC (2014).

However, there has been uncertainties in the direction of precipitation change depicted by the models, where precipitation is projected to decrease in some areas and increase in others (Martin et al., 2014). But, global precipitation records show an average increase in the frequency of wet days in some regions that include North America, Europe, and Southern Africa (Knapp et al., 2008). This increasing precipitation variability combined with livestock grazing pressure is likely to have future implications on degradation of rangelands since these two are among the main drivers of primary production in dry rangelands (Milchunas and Lauenroth, 1993, Koerner and Collins, 2014, Ruppert, 2014). For that reason, it is critical to understand how these ecosystems respond to the joint effects of increased drought frequency and intensity and grazing.

1.3.1 The African context

Africa is probably the most vulnerable continent to environmental change, given its proportionally large rural population whose livelihoods heavily rely on climate sensitive agricultural activities (Boko et al., 2007). For southern Africa, the effects of climate change are predicted to be greatest in northern regions, particularly the most arid parts (Gbetibouo and Ringler, 2009) where more aridification of the rangelands is predicted (Madzwamuse, 2010). While more than half of the land area in southern Africa is marginal, a large proportion of the population rely on rain-fed subsistence agriculture which is likely to be negatively impacted by future climate scenarios (Omari, 2010). For arid and semi-arid areas of southern Africa, rainfall reductions in the range of 5 – 10% for South Africa (Gbetibouo and Ringler, 2009, Madzwamuse, 2010) and up to 25% reductions in Botswana (Omari, 2010) have been predicted for the next 50 to 100 years. In addition, increased climatic variability and frequency of extreme events is forecasted for these areas.

In Botswana, 53% of the land area is used for livestock grazing (CAR, 2005) and 49% of the households rely on livestock husbandry for their livelihoods (Omari, 2010). This livelihood strategy is based on grazing of natural rangelands which are highly sensitive to climate variability. The vulnerability and sensitivity of these rangelands was demonstrated by the response to the El Niño-related droughts of the 1980s and 1990s where approximately 30% of the national herd was lost (Omari, 2010). It is the poorer small-scale farmers with fewer livestock that are likely to be affected the most. The areas that are most likely to be affected are those in the southwestern parts of the country (Kalahari) where annual precipitation ranges between 250 and 450mm, which is less than half the global annual average (GoB, 2001). Altogether climate change is expected to result in more frequent and severe droughts that hamper resilience leading to progressive rangeland degradation (Omari, 2010, IPCC, 2014).

Like Botswana, South Africa's livestock sector is also likely to suffer from the effects of climate change. Over 60% of agricultural land in South Africa is used for livestock grazing where more than 4.8 million small-scale farmers operate (Gbetibouo and Ringler, 2009). South African rangelands are expected to experience increasing frequencies of droughts and loss of grass-dominated ecosystems due to elevated CO_2 concentrations that result in an increase in woody vegetation cover (Madzwamuse, 2010). Increases in droughts, however, have devastating effects on the small-scale farmers whose herds tend to die from lack of water and nutrition (Madzwamuse, 2010). Thus, short-term mitigation strategies such as supplementary feeding are often used mainly to maintain and improve animal condition although this strategy has been blamed for worsening the problems of land degradation (e.g. Muller et al., 2015).

The savanna regions in the east and northestern parts of the country are likely to suffer forage losses of up to 20%, hence reducing the national herd by approximately 10% (Madzwamuse, 2010). Mean annual rainfall (about 450 mm) in these areas is almost half the global annual average (Ziervogel et al., 2014). The small-scale farmers in these regions particularly in the Limpopo and Eastern Cape provinces (Fig. 1.4) are most likely to be affected by climate change due to their heavy reliance on rain-fed agriculture and high poverty rate (Gbetibouo and Ringler, 2009).

This study sought to gain a better ecological understanding of the dynamics of livestock grazing in semi-arid rangelands of southern Africa faced with risks of climate and landuse change by evaluating: 1) effects of grazing intensity and grazing management system in the Kalahari rangelands of Botswana and 2) joint effects of climate change and grazing, and possible adaptation strategies through a precipitation manipulation experiment in Limpopo rangelands of South Africa.

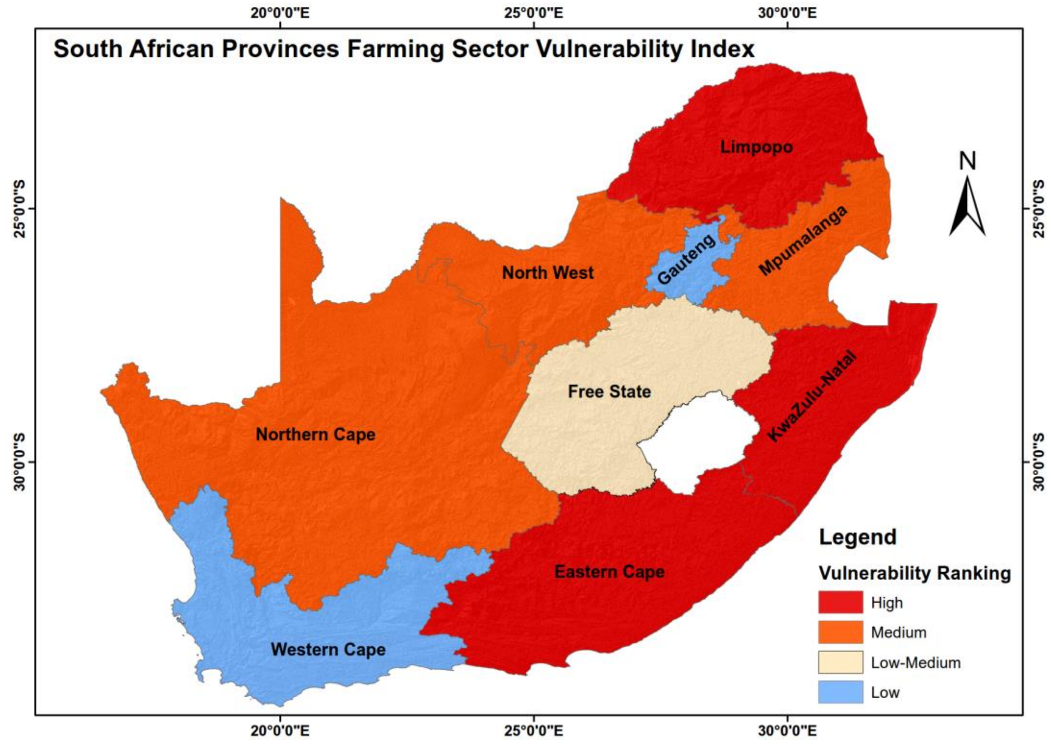

Figure 1.4: Map of South African farming sector vulnerability to climate change and variability. Modified from Gbetibouo and Ringler (2009).

1.4 Problem Statement

Livestock farming is by far the largest agricultural sector in the Limpopo province of South Africa claiming over 50% of the land surface as grazing land (Palmer and Ainslie, 2006). However, Limpopo is one of the three provinces that collectively have more than half the cattle population of South Africa. Hence, rangeland degradation in the form of reduced productivity, reduced soil fertility and soil erosion has been reported for this area (WWF, 2012). Poor veld conditions have been attributed to overstocking in conjunction with effects of climate change and the semi-arid nature of the region, all of which are thought to result in degradation or even desertification and permanent loss of productive land (Gbetibouo and Ringler, 2009). These pressures are expected to increase in future as a result of reduced rainfall and more frequent and severe droughts predicted for these areas (IPCC, 2014). Due to its lower adaptive capacity, triggered by highly populated rural areas dominated by small-scale farmers with high reliance on rain-fed agriculture, Limpopo is one of the most vulnerable provinces to the effects of climate change (Fig. 1.4; Gbetibouo & Ringler, 2009) Therefore, in order to improve the adaptive capacity of these ecosystems, an ecologically-oriented management that increases livestock production whilst maintaining or improving the stability and functioning of the ecosystem and preventing landscape degradation is required.

Although a substantial amount of grazing and drought research has been done globally, knowledge gaps still exist on the joint and interactive effects of these disturbances, particularly on the African continent. Grazing and drought experiments lack critical levels of realism and their results remain largely equivocal. Thus, novel empirical studies that explore in combination, the effects of drought and large herbivore grazing in

Limpopo are required. In the current study, a large-scale experiment that combines precipitation manipulations with cattle grazing and possible management options was conducted in the rangelands of Limpopo to complement plot and ranch-scale clipping and grazing studies conducted in semi-arid rangelands of southwestern Botswana.

1.5 Rationale

Global models predict that land degradation in drylands currently estimated at 10 – 20% is likely to increase as a result of climate change and human population growth (Reynolds et al., 2007, IPCC, 2014). These scenarios are expected to even have far reaching effects in African rangelands, particularly those with large rural populations relying mostly on subsistence livestock farming that thrive on natural grazing, such as in the Limpopo province of South Africa (Gbetibouo and Ringler, 2009). The major motivations were the predicted changes in the climate (i.e. reduced precipitation and increased frequency and intensity of droughts) and the livestock grazing system for these marginal areas, as well as the lack of adaptive capacity. From a purely scientific perspective, our limited knowledge on joint effects of drought and grazing, and hence a lack of science-based adaptation strategies to cope with increasing intensities and frequencies of drought, were an additional motivation. Thus, the results of this study provide insights that help advice policy and adaptive management, and mitigation strategies - such as supplementary feeding schemes both during and after droughts (Müller et al., 2015), to increase livestock productivity without compromising biodiversity in local rangelands and elsewhere.

1.6 Objectives

The overall aim of the study was to evaluate ecosystem functioning, service provision and ultimately suggest management options in grazed semi-arid rangelands faced with drought.

The specific objectives of the study were:

I. To determine joint effects of drought and grazing on the biotic and abiotic environment using a novel long-term large scale experiment that combines realistic large herbivore grazing with simulated drought.
II. To assess the effects of grazing frequency and extent of recovery periods on aboveground primary production using clipping (simulated grazing) experiments.
III. To determine influence of cattle grazing management systems on vegetation dynamics using ranch-scale case studies.

1.7 Research questions

The following questions were asked in order to address the research problem:

I. How can the knowledge gaps in drought and grazing (combined) studies be overcome in these ecosystems?
II. How does ranch-scale grazing management influence herbaceous and woody vegetation dynamics?
III. How does herbivore impact and recovery periods influence rangeland dynamics in climatically variable semi-arid ecosystems?

1.8 Thesis structure

The subsequent chapters of the thesis are structured as follows:

Chapter 2 is a review of literature relevant to the problem statement. The review focusses on previous conventional grazing and drought research in order to identify knowledge gaps particularly on questions relating to global environmental change.

Chapter 3 introduces the DroughtAct experiment which combines simulated drought and grazing treatments to evaluate ecosystem function and service provision from grazed and non-grazed vegetation under drought and ambient rainfall conditions. The experiment is a prototype in the new generation of drought experiments that include realistic treatments and hence is expected to bridge the information gaps identified in chapter 2. In addition to drought and grazing treatments, the study also evaluated possible management options under extreme conditions. The overall aim of the experiment was to determine if joint effects of drought and grazing were interactive or simply additive.

Chapter 4 presents an evaluation of grazing management systems from two ranch-scale case studies where in each case study, two adjacent ranches with different grazing management systems were compared. The aim of this study was to assess the long-term effects of continuous and rotational grazing on grassland and tree dynamics.

In Chapter 5, the effects of grazing frequency and extent of recovery periods on aboveground primary production was evaluated using clipping and dung addition treatments. The study also evaluated timing of recovery periods and response of palatable vs. unpalatable species. The aim of the study was to determine optimal time required by perennial grasses to recover from grazing events.

Chapter 6 presents a synthesis of the whole thesis including implications for management, policy and theory. The chapter also discusses limitations of the studies undertaken, grey areas for future research and general conclusions.

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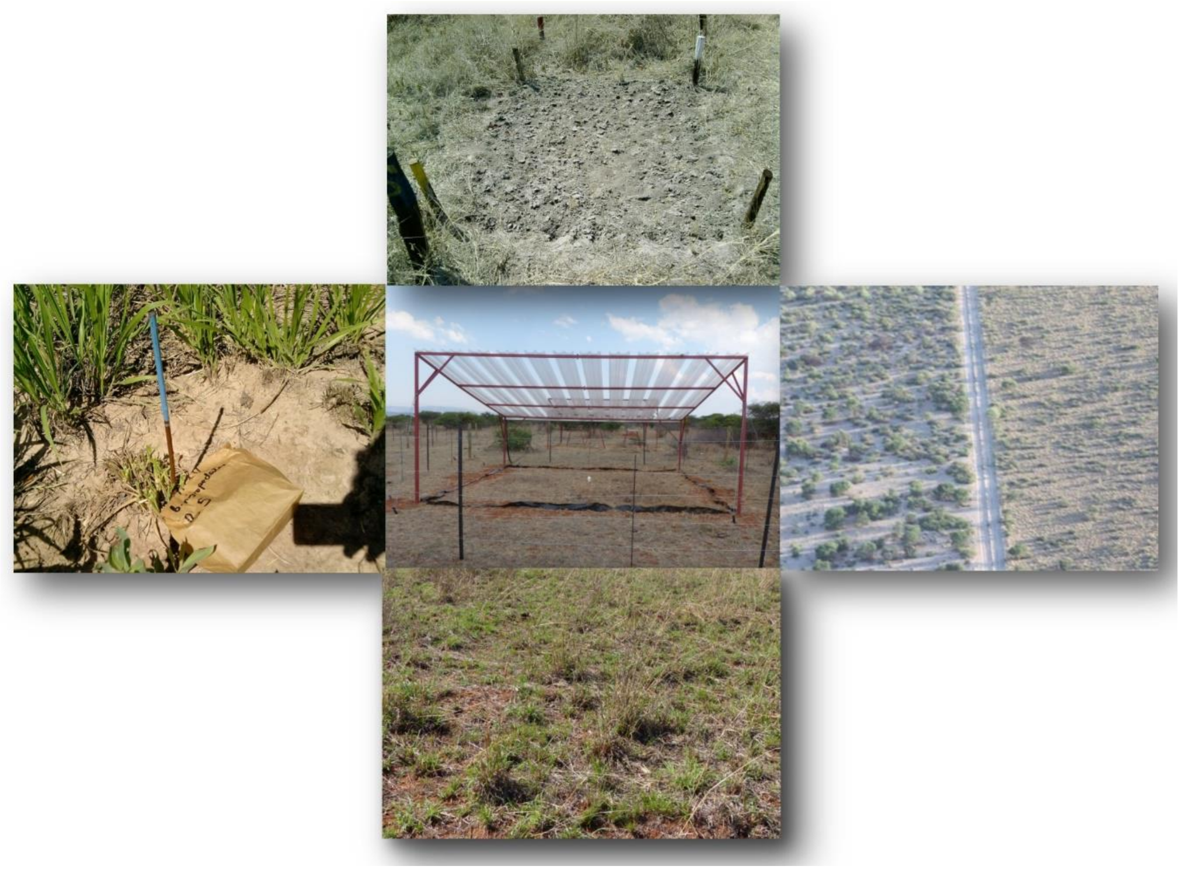
CHAPTER 2: Evaluating relevance of conventional grazing research under global change - A review of drought and grazing studies in semi-arid rangelands



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2.1 Introduction

Global environmental change has become a central theme dominating contemporary discussions and research on human and policy dimensions. This is because environmental changes have potential threats to food security and human health due to their influence on global food producing systems (Robinson et al., 2011). Among the set of global environmental change drivers, climate and landuse change are arguably the two most fundamental ones, and have the potential to change ecosystem structure and function (MEA, 2005a, Reynolds et al., 2007) depending on the intensity of the conditions and the resistance and resilience of the ecosystem (Hoover et al., 2014). Effects of global change are predicted to be devastating particularly in the African continent due to its vulnerability and low adaptive capacity (Boko et al., 2007).

In managed dryland ecosystems worldwide, changes in climate and landuse – usually assessed as changes in precipitation and grazing intensity, respectively – are the most important drivers of ecosystem change (D'Odorico et al., 2013, Delgado-Baquerizo et al., 2016). Livestock grazing is the most dominant landuse in these ecosystems where it provides livelihood security, be it on commercial scale or as subsistence practice (MEA, 2005a, Martin et al., 2016a). It occurs in an estimated 25 to 50% of the world's terrestrial area (Asner et al., 2004, Havstad et al., 2008). However, current global change models predict an increase in livestock numbers (MEA, 2005a, Reynolds et al., 2010) as a result of growing human populations; particularly in Africa (Robinson et al., 2011). Moreover, climate change models predict shifts in amount, frequency and seasonality of rainfall and an increase in frequency of extreme climatic events such as multi-year droughts (Knapp et al., 2008, Cherwin and Knapp, 2012, IPCC, 2014). These extreme climatic events together with increasing livestock numbers may hamper dryland ecosystem functioning and service provision (Gaitán et al., 2014, Ruppert et al., 2015).

In the light of these predictions, it should be scientific impetus to advance our understanding on how drylands will respond to future climate extremes and grazing scenarios, to invent sound mitigation strategies. A substantial amount of conventional research has focused on grazing strategies as management tools to avoid rangeland degradation and on vegetation responses to drought and grazing separately. However, to understand the potentially interactive effects of several global change drivers, the current gold standard is to simultaneously manipulate them in field experiments (Power et al., 2016, Alba et al., 2017). For this reason, this review assesses previous grazing and drought research in semi-arid rangelands with the aim of identifying strengths, limitations and knowledge gaps in both content and approach with reference to the African continent. In addition, this study seeks to provide evidence for contemporary thinking and recognize advances made towards mitigation of predicted global environmental change impacts.

2.2 Previous drought and grazing research

2.2.1 Grazing management strategies

Science-based grazing management, i.e. moving of animals across management units and/or landscapes in an effort to improve plant or animal performance, dates back as early as 1890s (Smith, 1895). To date, grazing managers and rangeland scientists continue to report mixed results from ranch-scale grazing strategies and small-scale experimental studies (Teague and Barnes, 2017). Two broad types of grazing strategies – continuous (CG) and rotational grazing (RG) have often been contrasted and compared.

Studies that compare grazing strategies are often inconsistent and have resulted in an unending debate on the superiority of either strategy. Most, but not all, grazing studies have concluded that RG is not superior to CG with respect to either range condition or animal performance (O'Reagain and Turner, 1992, Briske et al., 2008, Briske et al., 2011). In particular, Briske et al, (2008) concluded that recommendations supporting the superiority of RG over CG are based on anecdotal rather than scientific evidence. However, a growing body of literature provides examples of case studies and individual rancher experiences where RG has out-performed CG with regard to both vegetation condition and animal performance at larger scales (Barnes and Hild, 2013, Norton et al., 2013, Steffens et al., 2013, Teague et al., 2013, Wolf, 2016, Fynn et al., 2017, Odadi et al., 2017, Teague and Barnes, 2017). These studies put more emphasis on adaptive grazing management that allows for uniform and sufficient grazing and recovery times and assessments of the grazing impacts at appropriate ranch-scales.

Several reasons have been given for the contradicting results of experimental research and ranch-scale experiences. One overarching reason is that the temporal and spatial scales at which grazing experiments (as reviewed by Briske et al. 2008) are conducted, are unrealistically short and small, respectively (Teague et al., 2013). Moreover, grazing experiments usually apply rigid treatments as compared to adaptive strategies, hence, obtaining results contrary to those from adaptively managed RG ranches (Teague and Barnes, 2017). These authors further alluded that grazing experiments often lack to control for – or at least assess some key ecosystem drivers such as climate, management aspects (e.g. number of camps and stocking densities) and their interactions, and hence cannot easily be extrapolated to complex adaptive agroecosystems.

In a quantitative meta-analysis that included climate and management factors (number of paddocks, number of grazing days, size of grazing area and the experimental stocking rate) on the studies previously reviewed by Briske et al. (2008), Wolf (2016) discovered an increase in scale and an improvement in animal performance under RG. Furthermore, it is not easy to demonstrate the effects of grazing management from grazing experiments where animal movements are applied rigidly on small pastures that also lack plant species diversity (Barnes and Hild, 2013). Moreover, the designs of many fixed RG systems continually rotates livestock through paddocks of either grown-out low quality (over-rested) or insufficiently rested grass – a system that is at odds with the natural movements of grazing herbivores (Fynn, 2012, Steffens et al., 2013). Thus, it appears that the outcomes of experimental grazing studies are rather influenced by the often-overlooked experimental designs and management (Teague and Barnes, 2017).

While grazing management strategies (here: RG *vs.* CG) are already important in themselves for maintaining range condition and animal performance, their success also depends on stocking rates and its interplay with a given carrying capacity which is ultimately related to climatic, i.e. rainfall variability and amount. It is evident that stocking rate is an integral part of any grazing management strategy, where excessive stocking rates supersede management efforts (Briske et al., 2008, Fynn et al., 2017). Veld condition and carrying capacity is strongly affected by rainfall variability such that low rainfall or drought periods reduce carrying capacity (Fritz and Duncan, 1994) calling for adjustment of stocking rates to conservative levels that do not compromise grazing plans

(Fynn et al., 2017). Despite a growing amount of literature showing examples where RG systems out-performed CG systems, up until now, there is substantial uncertainty surrounding generalizations of response patterns observed.

2.2.2 Grazing research – grazing or simulated grazing (clipping)

Grazing research has existed for many decades worldwide. This research ranges from small-scale clipping experiments studies (Dyer et al., 1993, Turner et al., 1993, Hiernaux and Turner, 1996) to large-scale migratory ecosystems studies (McNaughton, 1979, McNaughton, 1985, Frank et al., 1998). Theoretical and empirical research in grasslands suggests that grazing may have positive (McNaughton, 1979, Frank et al., 1998), neutral (Knapp et al., 2012) or deleterious effects (Belsky, 1985) with respect to primary production. However, owing to their long evolutionary history with grazing herbivores, mesic grasslands have adapted well and often respond positively to grazing (Milchunas et al., 1988, Milchunas and Lauenroth, 1993). Thus positive response to grazing (also referred to as overcompensation), that is the capacity for regrowth to compensate for tissue loss (McNaughton, 1983, Augustine and McNaughton, 1998) often takes place in grasslands that have evolved with large herbivores and hence developed some tolerance to grazing (Milchunas et al., 1988, Del-Val and Crawley, 2005).

Apart from evolutionary grazing history, grazing effects may vary depending on the grazer i.e. generalist or specialist (Morris et al., 1992, Fynn, 2012), rate and intensity (Briske et al., 2008), spatiotemporal scales (Frank et al., 1998), prior rangeland condition (O'Connor et al., 2001) and timing of grazing events. Nevertheless, studies of clipping experiments have shown that defoliation may increase current season productivity but reduces productivity significantly in the next season (Turner et al., 1993). It is, however, acknowledged that, at high levels grazing generally reduces productivity irrespective of its temporal and spatial scales across landscapes.

Besides traditional ways of interpreting plant responses to grazing, there has been a shift towards a trait-based approach over the last decade (Diaz et al., 2007, Schellberg and Pontes, 2012, Wesuls et al., 2012, Linstädter et al., 2014). Plant functional traits help rangeland scientists to link plant morphological, physiological and phenological properties to their function in the ecosystem and hence can be useful indicators for rangeland condition (Schellberg and Pontes, 2012). This is because different species share traits that respond similarly to grazing disturbance (Jauffret and Lavorel, 2003). Thus, Diaz and colleagues (2007) proposed a set of traits (e.g. growth form, life history – annual *vs*. perennial, plant height and architecture) that may be used to measure plant responses to grazing pressure. Although the use of functional traits has gained substantial support worldwide, it is still difficult to find consistent, and thus generalizable, trait responses that could serve as grazing indicators across dryland biomes (Diaz et al., 2007, Linstädter et al., 2014).

In a global meta-analysis study involving several plant traits, Diaz et al (2007) found some inconsistent grazing responses across species growth forms (i.e. forb, graminoid, herbaceous legume or woody). For example, forbs and woody species showed neutral responses to grazing whereas graminoids responded either neutrally or negatively to grazing (Diaz et al., 2007). These response inconsistencies were linked to the broadness of the graminoid group in addition to a combination of precipitation and grazing histories.

Similarly, in a recent study in South African savanna and grassland biomes, Linstaedter et al. (2014) found no consistent trait responses to grazing across biomes, but only within a given biome, where some traits responded positively in the grassland and negatively in the savanna. These authors linked this finding to the convergent selective pressure of aridity and grazing (Quiroga et al., 2010) and suggested that traits with opposite responses to grazing in the two biomes may have a unimodal response along a gradient of additive pressures of aridity and grazing. Furthermore, Wesuls and colleagues (2012) found no relationship between growth form and plant height with grazing pressure and also warned that traits that respond to grazing may vary under different habitat conditions and also depending upon prevailing climatic conditions. Thus, while certain key traits that may help rangeland scientists understand and predict grazing effects have been identified, their responses may be variable in different climatic and historical contexts of global drylands.

2.2.3 Drought research – natural occurring and experimentally imposed drought

Research on experimental drought has existed and advanced for at least more than two decades (Jentsch et al., 2007, Knapp et al., 2008, Lloret et al., 2009, Cherwin and Knapp, 2012, Hoover et al., 2014, Tielbörger et al., 2014). Findings of experimentally imposed droughts (Fay et al., 2000, Fay et al., 2003, Grime et al., 2008, Plaut et al., 2012, Reichmann et al., 2013) reiterate and support documented ecological responses to naturally occurring droughts (Tilman and El Haddi, 1992, Zscheischler et al., 2014, Knapp et al., 2015, Copeland et al., 2016). For this reason, experimental droughts that make use of total (Reynolds et al., 1999) or passive rainout shelters (Yahdjian and Sala, 2002) to study ecosystems sensitivity to drought have gained popularity worldwide. Experimental droughts allow for stringent manipulation and/or control over other (confounding) environmental factors and hence disentangling drought effects from these (Hoover et al., 2018).

Evidence from studies that suffered anecdotal, unplanned droughts suggests that drought may have long lasting ecological consequences particularly on primary production (Zscheischler et al., 2014, Knapp et al., 2015) and plant community composition (Tilman and El Haddi, 1992). However, responses (as measured by primary productivity and community composition) from several drought sensitivity experiments have been variable (Byrne et al., 2017, Mulhouse et al., 2017, Sternberg et al., 2017, Wilcox et al., 2017). While Wilcox and colleagues (2017) found that aboveground net primary production was more sensitive to precipitation additions than reductions in drier ecosystems, Sternberg and colleagues (2017) found no precipitation legacies and negligible relationships with current season precipitation on peak biomass production in a Mediterranean grassland.

With respect to species composition in semiarid grasslands, Byrne and colleagues (2017) found neutral responses whereas Mulhouse and colleagues (2017) found a positive relationship between forb species richness and precipitation. The causes of variability have been attributed to local site differences related to soil properties and plant community composition (Hoover et al., 2018) and lack of coordinated research approaches and defined metrics of drought sensitivity (Smith et al., 2017). Thus far, patterns of ecosystem sensitivity to drought emerging from previous research are still largely ambiguous.

2.3 Limitations of previous research – the African context

Whereas grazing and drought research has become a large research focus globally, the African continent has been largely understudied, particularly with respect to drought research (Fig. 2.1). This hampers our knowledge about African ecosystems' sensitivity to combined effects of drought and grazing (Beier et al., 2012, Hoover et al., 2018). Of particular concern is the emerging evidence that the African continent is highly – potentially most – vulnerable to climate change (Boko et al., 2007). In addition, drought experiments imposing long-term (>4 years) and/or extreme droughts (>50% precipitation reduction) as projected for African drylands (IPCC, 2014) are lacking altogether.

Figure 2.1: Distribution of global coordinated drought experiments. The point indicates the location and size of the point indicates the number of experiments. Adopted from Hoover et al. (2018).

Contrary to drought research, grazing-related research is well established and documented in African rangelands. However, several limitations surround interpretation and extrapolation of grazing experiments results. Similar to drought experiments, most grazing experiments lack realistic temporal and spatial scales and often do not make good representation of real world scenarios. Moreover, most grazing experiments are too artificial as they used simulated grazing by clipping vegetation. Clipping lacks realism as it does not include other characteristics of herbivory such as selective grazing (Morris et al., 1992), hoof trampling and fertilization through dung and urine inputs (McNaughton, 1983). Studies that attempted to account for other herbivory factors (such as trampling and dung addition) in clipping experiments are limited.

Above all, short-term small scale grazing studies usually do not consider interactions with other elements of ecosystem function such as soil and climate properties, resulting in different and in most cases unsatisfactory outcomes when rigidly applied to larger scales (Teague et al., 2013). Despite a growing body of knowledge, suggesting the importance of multi-disciplinary approaches (see section below) to study complex interactions in managed ecosystems (Flombaum et al., 2017), studies that assess joint effects of drought and grazing are scarce. As a result, our understanding of the combined effects of drought and grazing in semiarid rangelands remains limited. Few studies have attempted to address these effects simultaneously, but they either used small-scale clipping experiments (Zwicke et al., 2013, Carlyle et al., 2014, Koerner and Collins, 2014), mowing treatments (Vogel et al., 2012) or grazing by sheep (Heitschmidt et al., 2005). Most of these studies were not located in Africa (although the study of Koerner and Collins included a site in Southern Africa) – where climate and evolutionary grazing histories are different.

Theoretical studies have also been used to explain the effects of aridity and grazing in drylands as convergent selective forces (Coughenour, 1985, Milchunas et al., 1988), but these original publications have not been sufficiently tested with empirical data. However, the convergence theory was confirmed in a field studies (Adler et al., 2004) and a common garden experiment (Quiroga et al., 2010). While these studies give relevant insights, they do not address the extremity of future climatic events as predicted by the global climate change models. Moreover, and similar to clipping experiments, common garden experiments using potted, isolated individuals are highly artificial as they neglect important community processes such as competition (and/or facilitation) and thus results need to be interpreted with caution and ideally should be repeated under more natural conditions.

Ruppert et al. (2015), used a meta-analytical approach to evaluate combined effects of drought and grazing across drylands worldwide. Although meta-analyses provide invaluable insights that could not emerge from single studies, these approaches also have limitations or can potentially suffer from several caveats when not performed with extreme caution. It lies in the nature of things that meta-analyses lack control over the levels of the treatments tested; they have to make sense of those treatments and level of treatments that are available. In more general terms, meta-analyses may suffer from publication bias or the *file drawer problem* where important studies may be excluded. In addition, when performed carelessly, meta-analyses may also mix studies that used incompatible approaches (“comparing apples and oranges”) and thus result in possible wrong conclusions (Eysenck, 1994).

Remote sensing and modelling techniques have also been used to estimate effects of rainfall variability and grazing in rangelands of southern Africa (Pickup, 1996, Dube and Pickup, 2001). Although these techniques provide good monitoring and early warning tools, they often need to be calibrated and validated with real field data. Besides, the usefulness of remote sensing data is limited in that specific vegetation responses such as shifts from perennial to annual herbage cannot be detected (see Dube and Pickup, 2001). Therefore, the lack of relevant drought experimental studies that include realistic grazing by large herbivores in southern African savannas do not only indicate presence of knowledge gaps in these grazed and drought-vulnerable regions, but also some limitations in international coordinated methodological approaches that allow comparisons of multi-site data that would improve understanding of these systems behavior under global environmental change.

2.4 Combined effects of drought and grazing – the need for multifactorial experiments

Complex ecosystems such as dry rangelands require multifactorial studies in order to understand the system behavior and predict possible responses under projected environmental change. Empirical evidence suggests that grazing often interacts with other environmental factors such as climatic variability to give variable responses in community composition and productivity (Suttle et al., 2007, Voigt et al., 2007, Post and Pedersen, 2008, Koerner et al., 2014). These interactions may either amplify (Voigt et al., 2007), mitigate (Post and Pedersen, 2008) or reverse (Suttle et al., 2007) climate change effects on trophic interactions, plant community composition, and several trophic levels, respectively. Koerner and colleagues (2014) also found that grazing interacted with increased rainfall variability to delay veld recovery.

Moreover, the strength and direction of interactive effects may vary for different proxies of ecosystem performance (Guuroh et al., 2018). For example, Guuroh and colleagues (2018) found that grazing reduced aboveground biomass but increased metabolizable energy. Altogether, the growing body of literature on combined effects of drought and grazing has underlined the complex nature of their interrelation and it is yet unclear whether these effects are simply additive or interactive (Zavaleta et al., 2003, Ruppert et al., 2015).

The convergence theory (Coughenour, 1985, Milchunas et al., 1988) suggests that both aridity and grazing are convergent selective forces and thus select for similar if not identical plant traits. Experimental results supporting the convergence theory were reported elsewhere (Adler et al., 2004, Quiroga et al., 2010), although Adler et al. (2004) also indicated the importance of interactions of grazing history with edaphic factors such as soil texture in the selection of plant traits. Furthermore, in a global data integration study, Ruppert et al. (2015) found that drought and grazing may interact in complex ways depending on vegetation characteristics such as the predominant plant life history.

Thus, it is evident that grazed ecosystems are complex and hence their response to droughts makes a strong case for experimental multifactorial studies that allow to assess effects of grazing and drought in isolation as well as in combination. In addition, effect strength and direction may be depended upon the assessed proxies of ecosystem performance (e.g. primary productivity, soil cover, plant functional traits, biodiversity), resting an additional case for the assessment of multiple ecosystem performance proxies within such multifactorial studies.

To measure individual and interactive effects of several global change drivers, the current contemporary approach is to simultaneously manipulate them in field experiments (Power et al., 2016, Alba et al., 2017). In this context, a rigorous and realistic experimental design is particularly important for understanding the response surface of ecosystem functions and services (Flombaum et al., 2017, Knapp et al., 2017), which is prerequisite for designing feasible adaptation strategies (Müller et al., 2015, Martin et al., 2016b).

2.5 Recommendations for future experimental approaches

As a way forward, and to contribute to a new generation of global change experiments, it is recommended that future global change researchers design large-scale multi-site field experiments that asses multiple determinants of ecosystem function and structure. Given the global nature of anthropogenic environmental change, ecological coordinated distributed experiments (CDE) that involve standardized and controlled protocols are needed to improve international collaborations and comparisons (Fraser et al., 2013). These would help correct the problems of methodological differences associated with meta-analytical studies.

In a drought and grazing experiment for example, the abiotic treatment (precipitation manipulation) should represent a centennial scale drought at that particular site and follow standardized protocols to make datasets comparable. In 2013, DroughtNet initiated the International Drought Experiments (IDE) with the aims of exploring terrestrial ecosystems' sensitivity to severe drought (DroughtNet, 2015). According to the IDE, precipitation amount and pattern is manipulated in realistic ways through the use of rain interception shelters (Yahdjian and Sala, 2002), based on a site’s past climatic characteristics (Knapp et al., 2017). In this way, the experiment adds realism in terms of site-specific rainfall scenarios (Thompson et al., 2013). Although the actual rainfall reductions differ across sites, the nature of the intended drought will be the same across all sites and thus keep the results more comparable than using a fixed rainfall reduction as done in the past.

As a result of the complexity of the combined effects of drought and grazing in drylands (Adler et al., 2004, Ruppert et al., 2015), it is crucial that multiple factors need to be assessed simultaneously. In this context, edaphic factors should be included and evaluated to determine their influence on the dynamics of drought and grazing. Soil properties are important determinants of plant production in drylands (Archer and Smith, 1972, Rezaei and Gilkes, 2005). But they are often influenced by climate (Delgado-Baquerizo et al., 2013) and disturbances such as grazing (Yong-Zhong et al., 2005, Jing et al., 2014), resulting in negative feedbacks on the resultant vegetation. Thus, in addition to the hypothesis of Milchunas et al (1988) as restated by Adler et al (2004), we propose addition of edaphic factors to the interactions of aridity and grazing (Fig. 2.2). We are convinced that edaphic factors play an important role in determining vegetation productivity and vigor and hence grazing resistance traits.

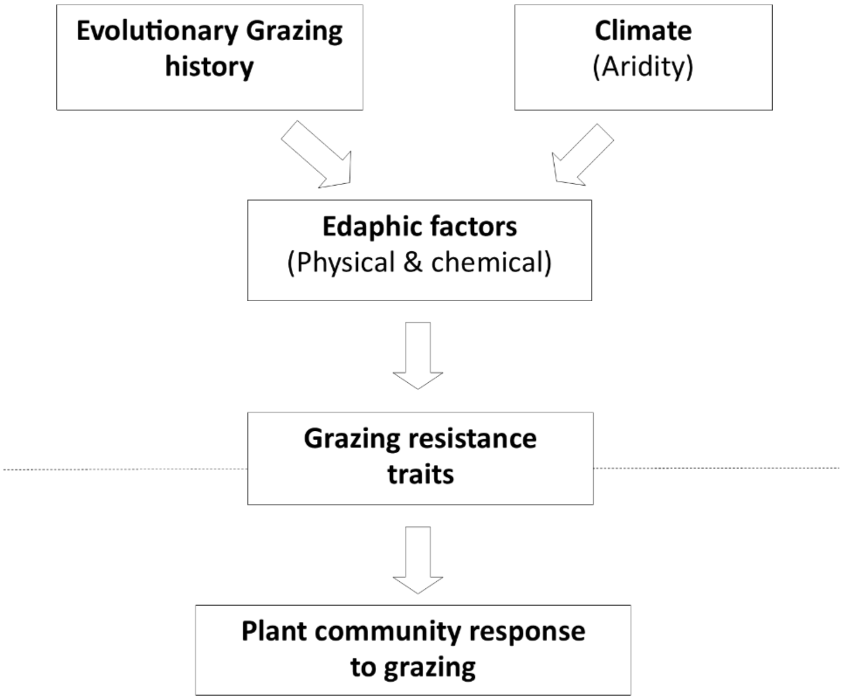

Figure 2.2: Proposed conceptual framework indicating the importance of edaphic properties (soil physical properties such as texture, and chemical properties such as carbon, nitrogen and phosphorus) on semiarid rangelands under climate change as per the convergence model. Modified from Adler et al. (2004).

For a biotic treatment, it is recommended that livestock be used to graze the experimental plots rather than simulated grazing. Using a factorial design, individual and combined effects of drought and large-herbivore grazing on ecosystems would be investigated. This approach brings novelty in the new generation of global change experiments, that go beyond respective climate change experiments by focusing on interactions of abiotic and biotic drivers (Power et al., 2016).

Furthermore, in order to evaluate the ecosystem’s sensitivity to drought (i.e. resistance and resilience to drought), a direct test of realistic management interventions through post-drought treatment changes is proposed. In a similar manner, grazing treatments may also be changed to mimic realistic grazing management scenarios under drought conditions such as resting / grazing during and after a drought to capture the grazing history effects hence assessing ecosystem recovery. However, to avoid tampering with the physical environment and creating an unwanted microclimate, particularly beneath the rainout shelters, it is imperative that controlled measurements of climatic factors that may influence plant growth dynamics (e.g. temperature, humidity, photosynthetic active radiation) and soil properties must be taken to separate artefact effects from treatment effects.

Thus the design of the rainout shelters should intercept rainfall while allowing free movement of grazing animals with minimum influence on the microhabitat. With this approach, multiple proxies of ecosystem performance such as aboveground net primary production, forage quantity and quality, soil properties and cover, community composition among others may be assessed. These kinds of multifactorial experiments are may solve the problems associated with previous drought and grazing studies while at the same time bridging the knowledge gap and research imbalance. For the African continent and particularly savanna drylands of southern Africa where grazing-related land degradation is common, such an approach would help increase ecological understanding of grazed ecosystems under climate change.

2.6 Conclusion

Whereas grazing and drought research have become global research foci, it was apparent that the African continent is still understudied particularly with respect to research on climatic extreme events such as drought. Drought research is not only limited in terms of the number of studies, but also with respect to realistic site-specific drought intensities and extent of the drought treatments (i.e. the duration of drought). On one hand, grazing research is well established and documented in African rangelands, at the same time these often lack realism with respect to temporal and spatial scales, the nature of treatments (e.g. clipping *vs.* grazing), experimental designs (common garden *vs.* in-situ manipulations) and multifactorial approaches that include further elements of ecosystem function such as soil properties. This lack of realism was identified as one of the main causes of inconsistencies in grazing research, what may partially explain the continuous debate on superiority of grazing systems.

However, we found few studies that used multifactorial approaches to study drought and grazing; either through theoretical analysis, meta-analysis, modelling and remote sensing, artificial grazing (clipping) or common garden experiments. As already mentioned, some of these studies lack realism and may need to be validated under more natural field conditions while some do not represent African rangelands due to different climate and evolutionary history of grazing. We further showed the need for rigorous and realistic multifactorial experimental designs that involve standardized and controlled protocols as well as site specific drought treatments, in order to bridge the knowledge gaps in African rangeland studies to overcome methodological problems associated with data integration and comparisons. Thus, present drought and grazing research and the state of knowledge does not adequately address future climate change scenarios predicted for southern Africa due to the limitations outlined above.

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CHAPTER 3: Adding realism and management options to global change experiments: the DroughtAct approach

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Abstract

Climate and land-use change are two pivotal drivers of global change in drylands. Current global models predict increasing rainfall variability, more frequent and intense droughts, and increasing livestock numbers particularly in African drylands. Given the livestock sector's heavy reliance on ecosystem services from rain-fed pastures in these regions, the projected changes have potential to impact ecosystem functions negatively. Here, DroughtAct is introduced, a novel approach that adds real grazing and post-drought treatments to conventional drought (passive rainout shelters) experiments, to evaluate grazed ecosystems' resilience and resistance to drought in a semiarid thornbush savanna of South Africa. A detailed implementation approach, bias check data, artefact and treatment effects and early vegetation responses are given. Neither site selection bias nor artefact effect on the biophysical environment were detected, but the drought treatment successfully reduced soil moisture. Vegetation responses showed reduced production with increasing rest periods, suggesting that, for veld in good condition prior to grazing, one season rest is optimal even under extreme drought conditions. Thus this setup provides an overview of ecosystem responses that can be measured using the experimental approach and is believed that the findings will contribute to solving the current 'experimental imbalance' in global change research.

Keywords: Ecosystem services, extreme events, grazing, rainout shelter, resting

3.1 Introduction

Climate and land-use change are two pivotal drivers of global change and may threaten ecosystem structure and function. In managed ecosystems worldwide, changes in rainfall and livestock grazing are among the most important drivers (D'Odorico et al., 2013, Delgado-Baquerizo et al., 2016). Current climate change models predict an increasing inter- and intra-annual variability in precipitation and thus an increasing frequency and intensity of climatic extreme events such as multiyear droughts (Knapp et al., 2008, Cherwin and Knapp, 2012, IPCC, 2014). Models further predict an increase in livestock numbers to meet the increasing human population in the 21st century and beyond (Reynolds et al., 2007). These extreme events have the potential to considerably impact ecosystem functions and services, but particularly in drylands (Gaitán et al., 2014, Ruppert et al., 2015).

Large herbivore grazing occurs in an estimated 25 to 50% of the world's terrestrial land area (Asner et al., 2004, Havstad et al., 2008). It may also have profound effects on ecosystem structure and function. Grazing may affect grassland productivity, whereas the net-effect mainly depends upon the spatial and temporal extent (Frank et al., 1998, Fynn, 2012, Teague et al., 2013), frequency and intensity (Briske et al., 2008), and timing of grazing (Chapter 5). Moreover, the evolutionary history of grazing in a given area plays a critical role (Milchunas et al., 1988). As a result, it is difficult to extrapolate grazing effects on ecosystem structure and function in space and time (Zwicke et al., 2013, Carlyle et al., 2014, Koerner et al., 2014).

Empirical evidence suggests that grazing often interacts with other environmental stressors and disturbances such as drought, further adding to variable responses

(Ceballos et al., 2010, He et al., 2011, Koerner et al., 2014). These interactions either increase (Voigt et al., 2007), reduce (Post and Pedersen, 2008) or reverse (Suttle et al., 2007) detrimental climate change effects on ecosystem performance; the strength and direction of interactive effects may even vary for different proxies of ecosystem performance (Guuroh et al., 2018). Drought and grazing effects may thus be additive or synergistic (Zavaleta et al., 2003, Ruppert et al., 2015). Unfortunately, combined effects of grazing and drought on ecosystem structure and function are even less understood than their individual effects. An important reason for our current lack of understanding is the limited number of studies exploring these stressors in combination and under controlled conditions (Flombaum et al., 2017).

Many studies have evaluated functional responses to grazing (Vesk and Westoby, 2001, Diaz et al., 2007, Linstädter et al., 2014) and drought (Knapp et al., 2008, Lloret et al., 2009, Cherwin and Knapp, 2012, Tielbörger et al., 2014) separately. The little knowledge we have about the combined effects of drought and grazing derived from small-scale field studies that simulated grazing via clipping (Zwicke et al., 2013, Carlyle et al., 2014, Koerner and Collins, 2014), from grazing history experiments along aridity gradients (Milchunas and Lauenroth, 1993, Adler et al., 2004, Quiroga et al., 2010), and from meta-analytical approaches (Ruppert et al., 2012, Ruppert et al., 2015). All of these approaches lack a certain amount of realism or control over either of the environmental drivers.

To assess interactive effects of several global change drivers simultaneously, the gold standard would be multifactorial field experiments (Power et al., 2016, Alba et al., 2017). In this context, a stringent and realistic experimental design is particularly important for understanding the response surface of ecosystem functions and services (Flombaum et al., 2017, Knapp et al., 2017b), which is a prerequisite for designing feasible adaptation strategies (Müller et al., 2015, Martin et al., 2016). To the best of our knowledge, though, the few field experiments that did address combined effects of grazing and drought (Zwicke et al., 2013, Carlyle et al., 2014, Koerner and Collins, 2014) lack this critical level of realism and/or experimental control. In particular, clipping experiments are highly artificial, as they omit effects of trampling (McNaughton, 1983), selective grazing (Morris et al., 1992) and nutrient addition through dung deposits (Chapter 5). Moreover, short-term small scale grazing studies usually do not incorporate all relevant ecosystem drivers nor their interaction, resulting in different and in most cases unsatisfactory outcomes when rigidly applied to larger scales (Teague et al., 2013). Likewise, meta-analytical studies lack control over tested treatment levels and may also be influenced by publication bias (Eysenck, 1994).

Here, DroughtAct, a large-scale long-term field experiment that assesses ecosystem responses to simultaneous effects of drought and large-herbivore grazing is introduced. DroughtAct is situated in a semi-arid savanna in South Africa’s Limpopo Province. This province has a particularly high rural population where livestock husbandry is the pivotal livelihood strategy, yet threatened by land degradation (Gbetibouo and Ringler, 2009). This makes it a relevant location for such an experiment. The drought treatment conforms to standards defined in the International Drought Experiments (IDE) (DroughtNet, 2015) – whereby drought intensities are objectively determined based upon a site’s specific rainfall characteristics (Knapp et al., 2017b). This places DroughtAct among a new generation of climate change experiments that incorporate realism in terms of rainfall scenarios (Thompson et al., 2013).

In going beyond respective climate change experiments, and to contribute to solving the current ‘experimental imbalance’ (Flombaum et al., 2017) in global change research, a true grazing treatment was added via a factorial design to investigate individual and combined effects of drought and large-herbivore grazing - thus incorporating realism (also) for biotic global change drivers (Power et al., 2016). A direct test of feasible and thus realistic management interventions was further added by introducing post-drought treatment changes after two and four years of drought. In this context, DroughtAct aims to explore grazed ecosystems’ resilience and resistance to drought; to evaluate if drought and grazing effects are additive (synergistic or antagonistic) or interactive; and to test possible rangeland management strategies in the face of drought.

This chapter details how to implement this approach, and presents pre-treatment data on biophysical conditions at the experimental site to check for bias. It further reports how experimental drought and grazing treatments affect the physical environment, including an artefact check of rainout shelters. Finally, data on selected vegetation responses to grazing exclusion is presented as a possible intervention strategy to avoid rangeland degradation in the face of drought (Müller et al., 2015). In focusing on the set-up and methodology, this chapter assists other researchers interested in establishing realistic, multi-factorial global change experiments. It specifically establishes DroughtAct as a prototype for combined grazing and drought experiments. The presentation of selected early results is intended to provide an overview of ecosystem responses that can be measured using this experimental approach.

3.2 Material and Methods

3.2.1 Study Site

The study was conducted on the experimental farm of the University of Limpopo, Syferkuil (23˚.8410’ S; 29˚.6950’ E), located in the Polokwane municipality of Limpopo Province, South Africa (Fig. 3.1). Syferkuil has a semi-arid climate with mean annual precipitation (MAP) of 489 mm and an inter-annual variability (1994 – 2016) of 32% (Fig. 3.1). Mean annual temperature is 19°C with summer maxima of 32°C and winter minima of 5°C (Syferkuil Weather Station 2017). The study period, 2013-2017 coincided with one of the strongest El Niño events in southern Africa in the past decades, with prolonged droughts over many provinces of South Africa (WMO, 2017).

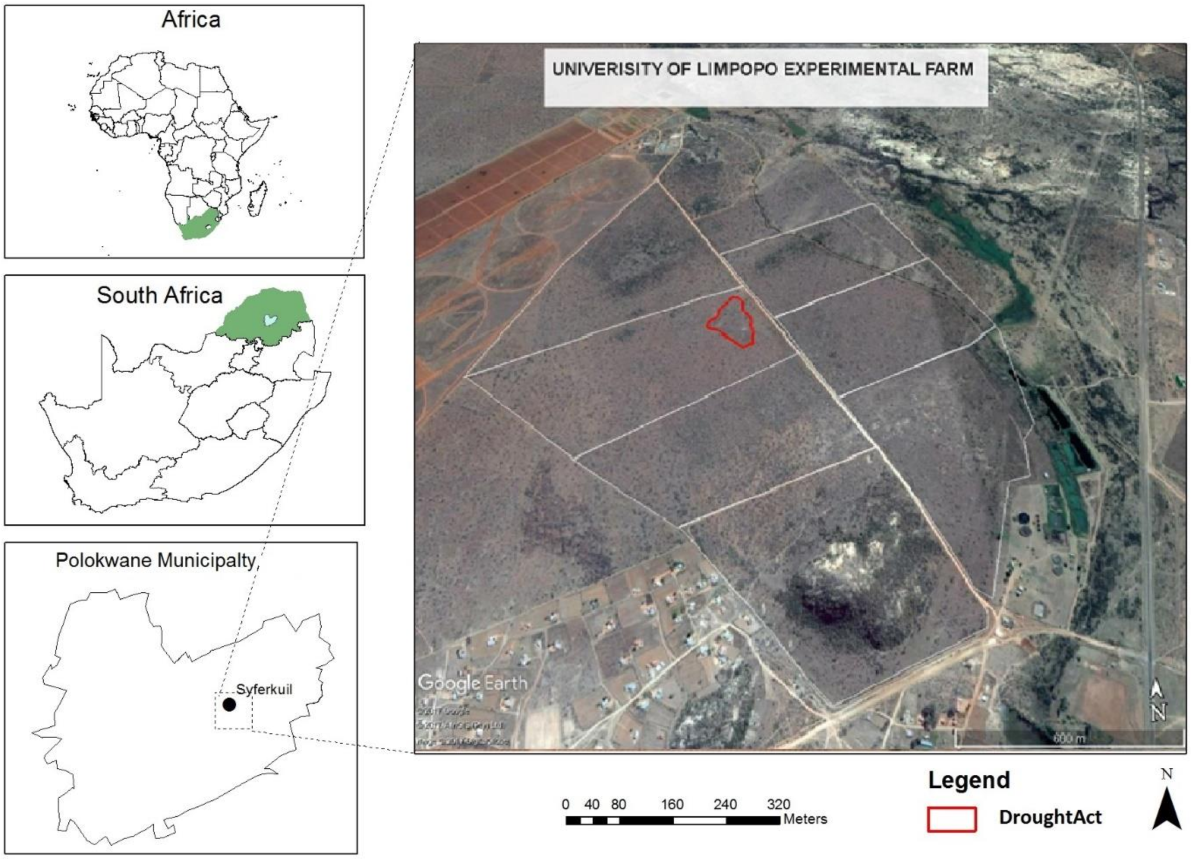

Figure 3.1: Map of study area location.

Soils are shallow sandy loams of the Glenrosa and Clovelly types (Group and Macvicar, 1991). Vegetation is an open thornbush savanna (Low and Robelo, 1996) belonging to the Pietersburg Plateau False Grassveld type (Acocks, 1994). The herbaceous layer is dominated by perennial C4 grasses such as *Themeda triandra*, *Digitaria eriantha*, *Schmidtia pappophoroides* and *Eragrostis* species, all of which have a good to moderate grazing value (Oudtshoorn, 1999). The woody component is dominated by *Vachellia tortilis* (Low and Rebelo, 1998).

The experimental camp (40 ha) was part of a rotational camp system (six camps, 280 ha), moderately grazed by cattle during the study period, 2013-2017 at a stocking density of 9 ha LSU^{-1} where an LSU is equivalent to a mature cow with a body weight of 450 kg (Meissner, 1983). Under the given management, grazing periods of the 25-30 animal herd did not exceed 30 days with intermittent recovery of not less than six or eight weeks during the growing and dry season, respectively. Management was established six years prior to the study period, resulting in good veld condition at the onset of the experiment. See Appendix S3.1 for details of grazing management.

3.2.2 The DroughtAct Design

3.2.2.1 Treatments

In December 2013, experimental blocks and plots were demarcated but still kept under regular moderate grazing management prior to treatment implementation, in order to test for selection bias (cf. 2.3). Blocks (four blocks of 40 x 40 m, with a minimum distance of 40 m) were arranged along a grazing gradient away from a watering point with block A closest (~30 m) whereas blocks C and D were furthest (~150 m) from the watering point. Each block was divided in nine 10 x 10 m plots (with 5 m corridors between plots) arranged in a three by three grid.

Experimental treatments were only established at the end of the dry season in October 2014, in a fully randomized factorial block design to control for potential spatial variation (Fig. 3.2). Grazing treatment (G) with two levels: grazed (G+) *vs.* resting (grazer exclusion; G-). Precipitation treatment with two levels: Ambient rainfall (D-) *vs.* drought (66% rainfall reduction; D+). In each block we combined and replicated the four treatment combinations: grazing exclusion (resting) in ambient rainfall conditions (**G-D-**), resting under drought conditions (**G-D+**), grazing under drought conditions (**G+D+**), and the control - grazing under ambient rainfall (**G+D-**) (Fig. 3.2).

The in-block (pseudo-)replicates were not established to serve as fully independent replicates but to be standby plots that would undergo a treatment change in a third season (2016/17) mimicking potential realistic management interventions (Fig. 1). Thus, using this design, for two seasons (2014/15 to 2015/16) we had four blocks with four treatment combinations (pseudo-) replicated twice per block, making a total of 32 plots (*n* = 32). However, in the 2016/17 seasons we implemented our treatment changes on the in-block replicates, adding four post-drought / grazing treatments; post drought and continued resting (**D+^{p} G-**), post drought and post grazing (**D+^{p}G+^{p}**), post drought and continued grazing (**D+^{p} G+**), continued ambient conditions and post grazing (**D- G+^{p}**), resulting in a total of eight treatments per block. Data on treatment changes is not presented in this chapter.

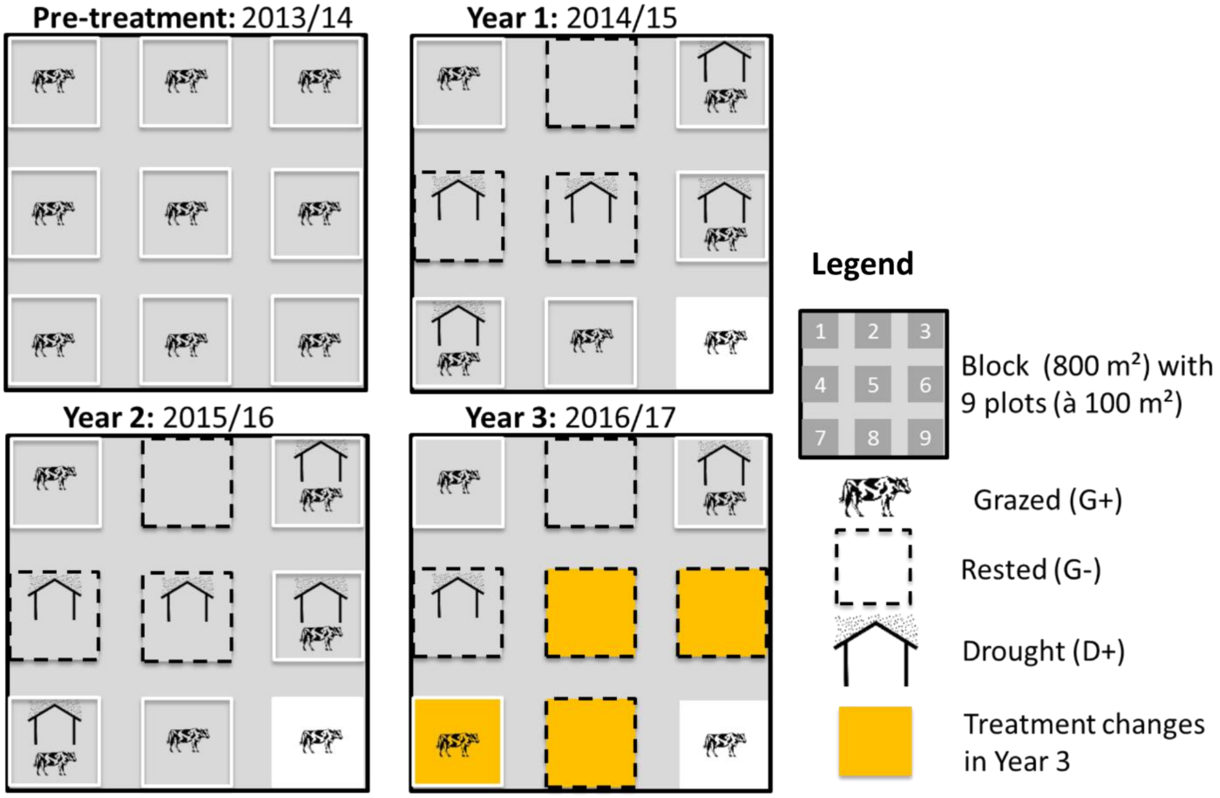

Figure 3.2: The DroughtAct experimental design, a randomized complete block design showing a grazed pre-treatment year, followed by two years of unchanged treatments of; grazing (G+), resting (G-), drought (D+), ambient (D-) replicated in four blocks with eight plot with eight plots each, and a third year of treatment changes for evaluation of drought resistance and resilience. The treatment changes involved removal of drought (drought history) and erection of fences (grazing history). The ninth plot was not used in the treatment years.

3.2.2.2 Making a Drought: Rainout shelters and Trenches

To simulate drought, we constructed permanent fixed-location 6 m x 6 m passive rain out shelters. The shelters were constructed according to the design of Yahdjian and Sala (2002) with modifications in size and height to allow cattle to roam and grazing underneath. The angled shelter roofs, 3 m and 2 m from the ground at the up and down slope, respectively, were made from polycarbonate (PC) transparent plastic sheets (Fig. 3.3). Gutters and downpipes were installed on the down slope side of the shelters to drain water away from the drought plot and neighboring plots. Our shelters were designed to reduce incident precipitation by 66%, mimicking a centennial-scale drought at our site (i.e. a drought with a 1% occurrence-probability given site's rainfall history), following the standards of the IDE protocol.

To decouple drought plots from lateral ambient soil water movement, we trenched around the perimeter of the shelter to maximum soil depth (≤ 70 cm) and inserted an impermeable plastic membrane. We also made our sub plots smaller (4.8 m x 4.8 m) than the shelter to give a 60-cm buffer between the edge of the plot and that of the shelter, hence reducing edge effects. We further oriented shelters to intercept rain from the dominant wind direction (Carlyle et al., 2014).

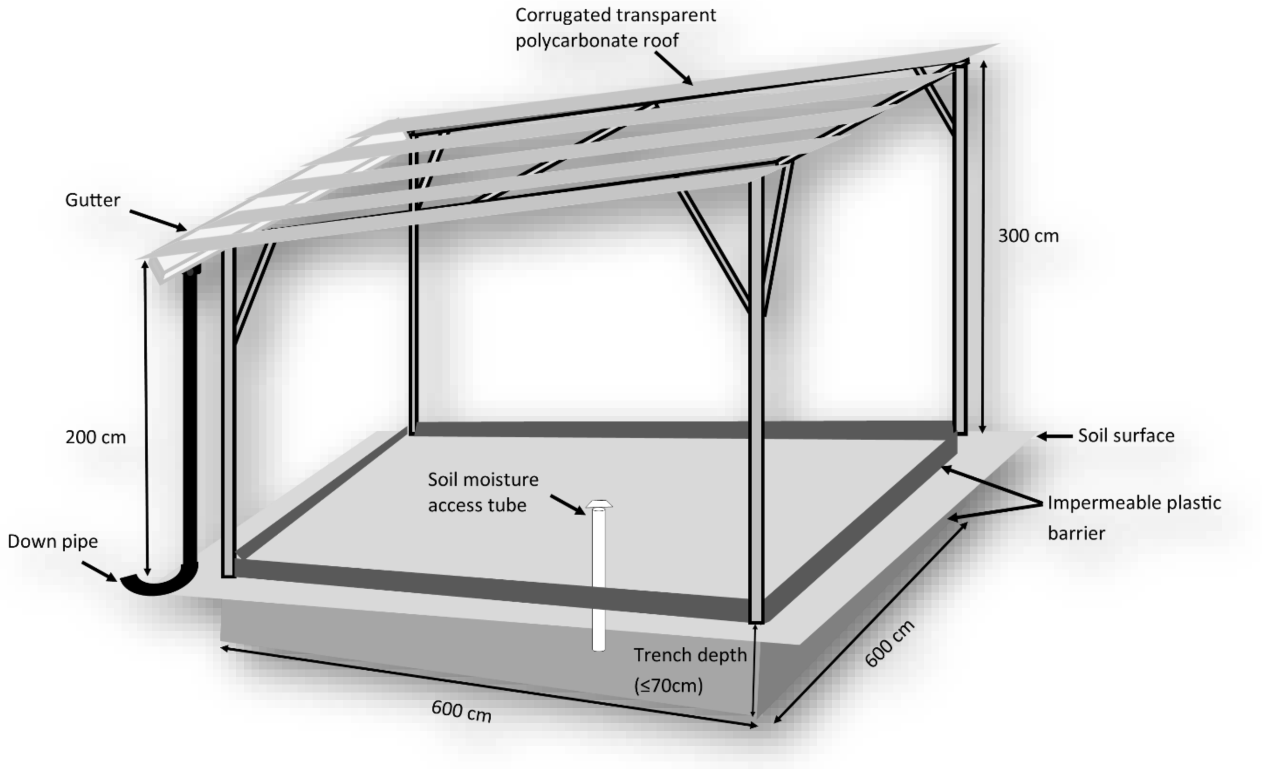

Figure 3.3: Schematic of rainout shelter design at DroughtAct experiment.

3.2.2.3 Grazing and Grazing Exclusion

At each block, three 10 m x 10 m fenced long-term grazing exclosures (LTE), one under ambient conditions and two under drought conditions were constructed. The exclosures were constructed to avoid cattle grazing (five strands of high strain wire) but may not completely prevent game grazing. Exclosures were erected at the end of the 2013/2014 dry-season (September / October 2014). Three permanent 1 m^2 quadrats were demarcated within the subplot for vegetation assessments.

The remaining five plots per block, three under simulated drought and two under ambient rainfall conditions were left open to allow grazing by cattle. We placed three paired quadrats in each plot where in each pair there was a 1.2 x 1.2-m moveable short term grazing exclosure (STE) cage and a permanent 1 m^2 grazed (GRA) quadrat (Fig. 3.4). Prior to installation of the cages we mowed the biomass on the cage positions before anchoring them down with steel pegs. This step was necessary to validate subsequent aboveground net primary production (ANPP) estimated via the peak standing crop method (Scurlock et al., 2002, Ruppert and Linstädter, 2014) where uniform starting points are attained by removing residual biomass and carryover material from the previous year. While, the GRA was continuously grazed for subsequent seasons without rest, the STE was moved to different positions around the GRA plot each season. This paired quadrat design allowed to quantify grazing offtake (GO, i.e. the difference between standing biomass between STE and GRA).

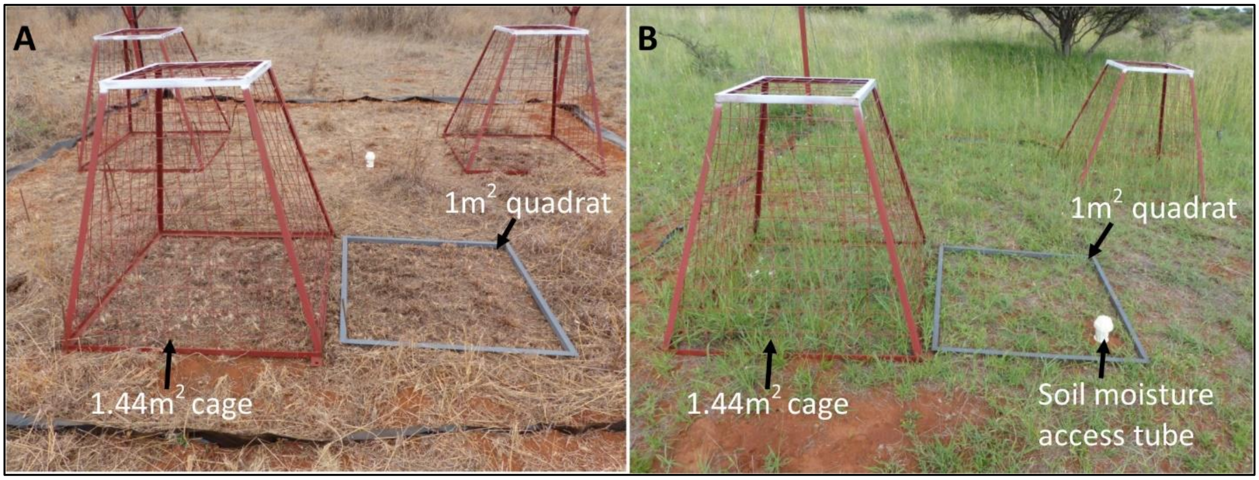

Figure 3.4: An illustration of the arrangement of paired short term exclosure (STE) cages and grazed (GRA) quadrats on a grazed plot subject to drought. Photographs (from different plots) were taken immediately after plot preparation at the end of the growing season in October 2014 **A**, and during the growing season in January 2015, **B**.

3.2.3 Quantification of selection bias and treatment artefacts

3.2.3.1 Selection bias check

To describe baseline site characteristics and to check for selection bias, we collected data on biophysical conditions across all plots in the pre-treatment year, i.e. in the vegetation season before experimental treatments were established.

With respect to vegetation, we measured aboveground biomass, vegetation composition, basal cover and diversity (species richness, species diversity and evenness). Aboveground biomass was collected plot-wise within a grazing exclusion cage (120 x 120 x 120 cm). Cages were installed during the onset of the 2013/2014 vegetation season, by clipping all standing biomass to stubble height (ca. 5 cm). At peak standing biomass (April 2014), all plant material grown within the center 1 m^2 area of each cage was clipped to stubble height, collected, oven-dried at 60°C for 48 hours and weighed to the nearest gram (Scurlock et al., 2002, Ruppert and Linstädter, 2014).

Vegetation composition, basal cover and diversity, were assessed via the line intercept method (Canfield, 1941, Rochefort et al., 2013). We sampled along five parallel lines marked with steel pegs at the ends, 120 cm apart and 480 cm long in each plot (23 m^2) divided into 16 equal 120 x 120 cm quadrats. One of the 16 quadrats would be left as a spare. Species richness (*S*) was assessed on whole plot level (23 m^2). Species diversity (*H*`) and evenness (*E*) were assessed using Shannon's and Pilou's indices, respectively, based upon cover records from line intercept.

As physical conditions, we measured soil moisture, soil physiochemical properties and rainfall (onsite weather station). In each plot a single soil moisture access tube for in situ volumetric soil moisture measurements was installed (36 in total including spare plots). Measurements were recorded weekly at 10 cm depth intervals (maximum depth ≤70 cm; Diviner 2000, Sentek Technologies), from December 2013 and continued into subsequent treatment seasons. We also collected three pooled 5 cm diameter topsoil (0 - 5 cm) core samples from random positions (off the parallel lines) on the subplots.

Soil chemical and texture analysis were carried out at the University of the Free State Soil Science laboratory using standard methods (Committee, 1990). Soil particle size distribution was determined with the sieve and pipette method and the soil texture classification is according to the United States Department of Agriculture (USDA) classification. Soil pH was determined in a 1:2.5 soil to water suspension. Extractable P was measured with Olsen's extraction. Exchangeable cations (Ca, Mg, K and Na) and Cation Exchange Capacity (CEC) were determined by atomic absorption at pH 7 with 1 mol dm^{-3} NH_4OAc and 1 mol dm^{-3} NaOAc, respectively. Total N and total C were determined by Leco combustion. Extractable micronutrients (Cu, Mn, Fe and Zn) were determined by the diethylenetriaminepentaacetic acid (DTPA) method (Lindsay and Norvell, 1978).

3.2.3.2 Treatment artefact check

Since implementation of the treatments, biophysical site conditions were monitored and a number of measurements were taken to evaluate shelter effects on the microhabitat. Light transmittance was assessed by measuring photosynthetic active radiation (PAR) using a pair of Apogee quantum meters (MQ-200) with a separate sensor beneath and outside the shelter. PAR measurements (30 minute averages) were taken for 48 hours in each month (January, February and March 2015). In March 2015, a pair of TinyTag Plus2 loggers (TGP-4500) were installed in each block, one beneath and the other outside a shelter, to measure temperature and relative humidity at hourly intervals.

3.2.4 Treatment effects

3.2.4.1 The physical environment

Treatment effects on the physical environment were assessed by measuring drought intensity, soil moisture dynamics and soil physiochemical properties. The standardized precipitation index (SPI) was used to assess drought intensity (McKee et al., 1993) under ambient and experimental drought conditions. The SPI is a widely used and accepted precipitation index in ecological studies (Vicente-Serrano et al., 2012, Ruppert et al., 2015). The SPI values were calculated for precipitation sums of each hydrological year at the experimental site. In order to assign drought intensity values to SPI classes, the classification approach of the National Drought Mitigation Centre of the USA (NDMC,

2017) was used. For more information on drought intensity and SPI classification refer to Appendix S3.2.

We evaluated soil moisture dynamics from 30-cm soil moisture sensor probes (Sentek EasyAG Version 3.1) with their data loggers (EnviroScan Solo Version 1.4), installed near the center of the plot, one beneath and the other outside the shelter per block. The sensors, installed in November 2015, measured hourly soil moisture at 10-cm depth intervals and complemented the Diviner 2000 measurements. We further carried out soil sampling and subsequent laboratory analysis in September 2016 following the same procedure used in the pre-treatment year. However, soil profile sampling was carried out on four pits per block (12 in total), each pit dug on the 1-m^2 spare quadrat within the subplots of the main treatment plots.

3.2.4.2 Vegetation characteristics

To determine treatment effects on vegetation dynamics, we quantified aboveground net primary productivity (ANPP) according to the peak standing crop method using both destructive and non-destructive biomass sampling (Scurlock et al., 2002, Ruppert and Linstädter, 2014). We sampled at the end of the growing season (April to May) in 2015, 2016 and 2017. On grazed plots, ANPP was harvested from moveable cages, whereas in rested plots we sampled standing biomass non-destructively using allometric equations (biovolume) (Scurlock et al., 2002, Lauenroth et al., 2006, Ruppert and Linstädter, 2014). The difference between ANPP and standing biomass was considered grazing offtake (GO) and was used to assess variability in grazing pressure across plots and blocks. Prior to harvesting, we measured average plant height (≤ 5 individuals) and estimated percentage total canopy cover for each species. Canopy cover was also classified into live material (green plus senescent) and previous year's standing dead material (grey and oxidized). We also estimated quadrat-level cover of litter, bare ground and other material such as dung and stones.

3.2.5 Statistical Analysis

The data were analyzed in three steps using linear mixed effect models tested with ANOVA. First we assessed selection bias across our blocks on pre-treatment data using plot as random and block as fixed effect in the model. For dynamics in soil moisture, we performed repeated measures ANOVA based on weekly soil moisture readings across the entire growing season. Secondly, we quantified artefact and treatment effects by computing response ratios (ambient : shelter) on PAR, temperature, relative humidity, GO and soil moisture followed by two sample *t*-tests to determine significance of the effect. Lastly we tested treatment effects on plant canopy cover by using repeated measures ANOVA (Type II) with time (season) and drought as fixed effects and block as a random factor. Residuals were checked for homogeneity of variance according to standard protocols (Zuur et al., 2010). Where necessary, data were ln-transformed to fulfill ANOVA assumptions. Where significant effects were detected, we further computed Tukey multiple comparisons. All statistical analyses were performed in R, version 3.3.1 using packages *nlme* and *ggplot2* (R Core Team, 2016).

3.3 Results

3.3.1 Pre-Treatment Biophysical Conditions

Data collected during the pre-treatment season did not render any signs of systematic selection bias. Vegetation was homogeneous across blocks with respect to standing biomass, basal cover as well as diversity (Table 3.1). Also physical and chemical soil parameters were relatively homogeneous across blocks. Soils did not differ with respect to texture and bulk density, but with respect to soil depth, which also translated to slightly variable soil moisture contents across the top 30 cm of the soil. Block C, the shallowest, tended to have slightly higher soil moisture during the pre-treatment season (wet and dry season; Fig. 3.5). However, block C was not significantly wetter than block D and block B at depths 10 and 30 cm, respectively ($P > 0.05$). Soil chemical properties were slightly more variable, however, differences were marginal. Soil pH was highest on the shallowest Block C. Total N and extractable Zn were lower at block D.

Table 3.1: Site characteristics (mean ±SE) of the four experimental blocks at DroughtAct measured during the pre-treatment year from December 2013 to October 2014.

State	Parameter		Block A	Block B	Block C	Block D
Biotic	Standing biomass (g m^{-2})		105.9 ± 7.89	104.0 ± 11.6	109.7 ± 15.5	113.9 ± 18.5
	Basal cover (%)		31.20 ± 2.27	27.16 ± 1.52	29.07 ± 2.48	27.23 ± 2.73
	*Shannon index *H`*		1.43 ± 0.08	1.360 ± 0.12	1.40 ± 0.16	1.61 ± 0.13
	*Evenness *E*		0.74 ± 0.03	0.741 ± 0.05	0.73 ± 0.03	0.78 ± 0.04
	*Species richness *S* (no. $23m^{-2}$)		7.00 ± 0.53	6.253 ± 0.49	7.00 ± 0.98	8.13 ± 0.67
Abiotic (physical)	Soil maximum depth (cm)		47.78 ± 6.19a	50.00 ± 5.27a	22.22 ± 3.64b	33.33 ± 5.27a
	Clay (%)		7.70 ± 0.41	7.58 ± 0.27	8.03 ± 0.32	7.11 ± 0.28
	Silt (%)		11.58 ± 0.43	11.86 ± 0.32	13.33 ± 0.41	12.61 ± 0.77
	Sand (%)		79.44 ± 0.72	79.04 ± 0.38	77.56 ± 0.31	79.10 ± 0.47
	Bulk density (g cm^{-3})		1.46 ± 0.02	1.44 ± 0.02	1.30 ± 0.02	1.53 ± 0.02
	Soil moisture (%)	-10 cm	40.70 ± 0.97a	39.76 ± 0.64a	44.94 ± 1.98b	44.09 ± 1.33ab
		-20 cm	46.49 ± 1.42a	46.63 ± 0.66a	53.28 ± 2.03b	49.33 ± 1.52a
		-30 cm	52.70 ± 1.45a	53.12 ± 1.32ab	60.55 ± 3.71b	53.26 ± 1.77a
Abiotic (chemical)	pH		6.08 ± 0.04a	6.07 ± 0.02a	6.28 ± 0.09b	6.09 ± 0.05a

Extractable P (x10^{-3} mg g^{-1})	3.11 ± 0.14	3.51 ± 0.35	3.19 ± 0.33	3.11 ± 0.20
Total N (mg g^{-1})	0.82 ± 0.04ab	0.84 ± 0.03a	0.80 ± 0.03ab	0.70 ± 0.05b
Total C (mg g^{-1})	7.09 ± 0.45	7.69 ± 0.31	7.13 ± 0.23	7.19 ± 0.73
NaCEC (cmol g^{-1})	1.13 ± 0.08	1.20 ± 0.08	1.07 ± 0.04	1.05 ± 0.06
Extractable Cu (x10^{-3} mg g^{-1})	1.35 ± 0.06	1.41 ± 0.04	1.44 ± 0.02	1.38 ± 0.0
Extractable Mn (x10^{-3} mg g^{-1})	41.87 ± 3.57	43.04 ± 4.54	47.41 ± 5.51	42.22 ± 3.97
Extractable Fe (x10^{-3} mg g^{-1})	15.87 ± 1.09	16.71 ± 0.76	13.84 ± 0.41	14.35 ± 1.30
Extractable Zn (x10^{-3} mg g^{-1})	0.84 ± 0.01ab	0.93 ± 0.01a	0.73 ± 0.01ab	0.65 ± 0.004b

Soil physical (except moisture) and chemical properties are from the top soil (0 – 5 cm). Different letters in a row indicate significant differences ($P < 0.05$) between the blocks based on Tukey multiple comparisons tests.

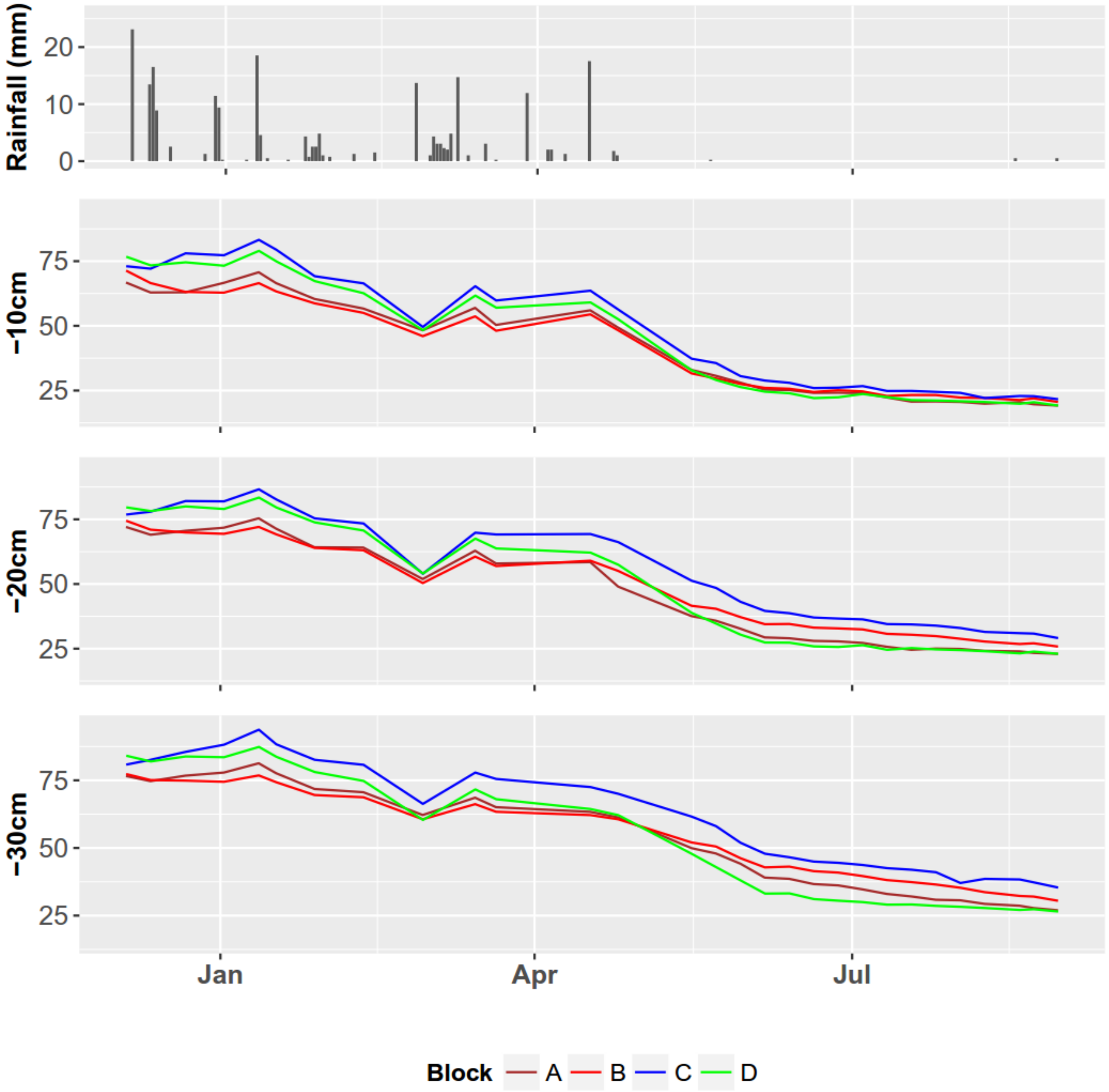

Figure 3.5: Temporal trends in precipitation and percentage soil moisture at three depths measured at DroughtAct during the pre-treatment year from December 2013 to September 2014.

3.3.2 Artefact check: Monitoring treatment effects and unintended artefacts

To assess treatment success as well as potentially (unintended) treatment artefacts, several biophysical parameters were monitored throughout the duration of the study.

Effects of the rainout shelters were highly specific, in the sense that they reduced soil moisture but did not alter any other of the tested biophysical parameters related to plots' microclimate or in relation to the grazing treatment.

Photosynthetic active radiation (PAR), air temperature, relative humidity as well as grazing offtake (GO) were not affected by the rainout shelters (Table 3.2). However, available soil moisture, i.e. the intended treatment effect, was significantly reduced across the soil horizon ($P < 0.001$, Table 3.2, Fig. 3.6). Temporal soil moisture trends in both drought and ambient conditions showed prominent oscillations with precipitation at 10cm depth category while drought oscillations became less prominent at deeper layers (Fig. 3.6). Grazing did not influence soil moisture at all depth categories (results not shown).

Given the passive nature of our rainout shelters, drought intensity is directly depended upon the ambient rainfall conditions in a given season. To assess drought intensity in a standardized fashion, we also classified ambient precipitation during a season as well as a drought plot's precipitation by means of the standardized precipitation index (McKee et al. 1993; Fig. 3.7). Altogether, the intended drought intensity (exceptional drought, i.e. centennial-scale drought) was met in all season. Whilst plots under ambient rainfall conditions faced severe drought, normal rainfall and abnormally dry conditions in seasons 2014/15, 2015/16 and 2016/17 respectively, plots under drought treatment faced exceptional drought conditions throughout the study period (Fig. 3.7).

Table 3.2: Rainout shelter effects (artefact checks) on photosynthetic active radiation (PAR), minimum and maximum temperature, relative humidity, grazing offtake and drought effects on soil moisture at 10 – 30 cm depths, at the DroughtAct.

		Ambient (D-)	**Shelter (D+)**	**% Diff**	**Df**	***t* value**	***P* value**
PAR (mg mol^{-1})		1117.6	965.2	13.6	159	1.43	0.15
Max.Temp (°C)		33.3	33.6	-1.1	431	0.56	0.57
Min.Temp (°C)		7.7	7.8	-1.6	431	0.14	0.89
Relative humidity (%)		61.9	61.4	0.9	431	0.52	0.30
Grazing offtake (g m^{-2})		64.9	57.8	10.9	108	0.67	0.50
Soil moisture (mm)	10cm	9.4	4.4	52.5	21631	73.05	***
	20cm	8.7	6.3	27.2	32054	72.96	***
	30cm	10.0	8.0	19.6	22877	46.6	***

*< 0.05, ** < 0.01, *** < 0.001.

Measurements were taken at different times during the study period (2014 to 2017). The *t* and *P* and degrees of freedom (Df) values are from two sample t-tests. Soil moisture data presented here is average hourly readings from the EasyAG probes installed on D+ and D- plots during the first treatment year.

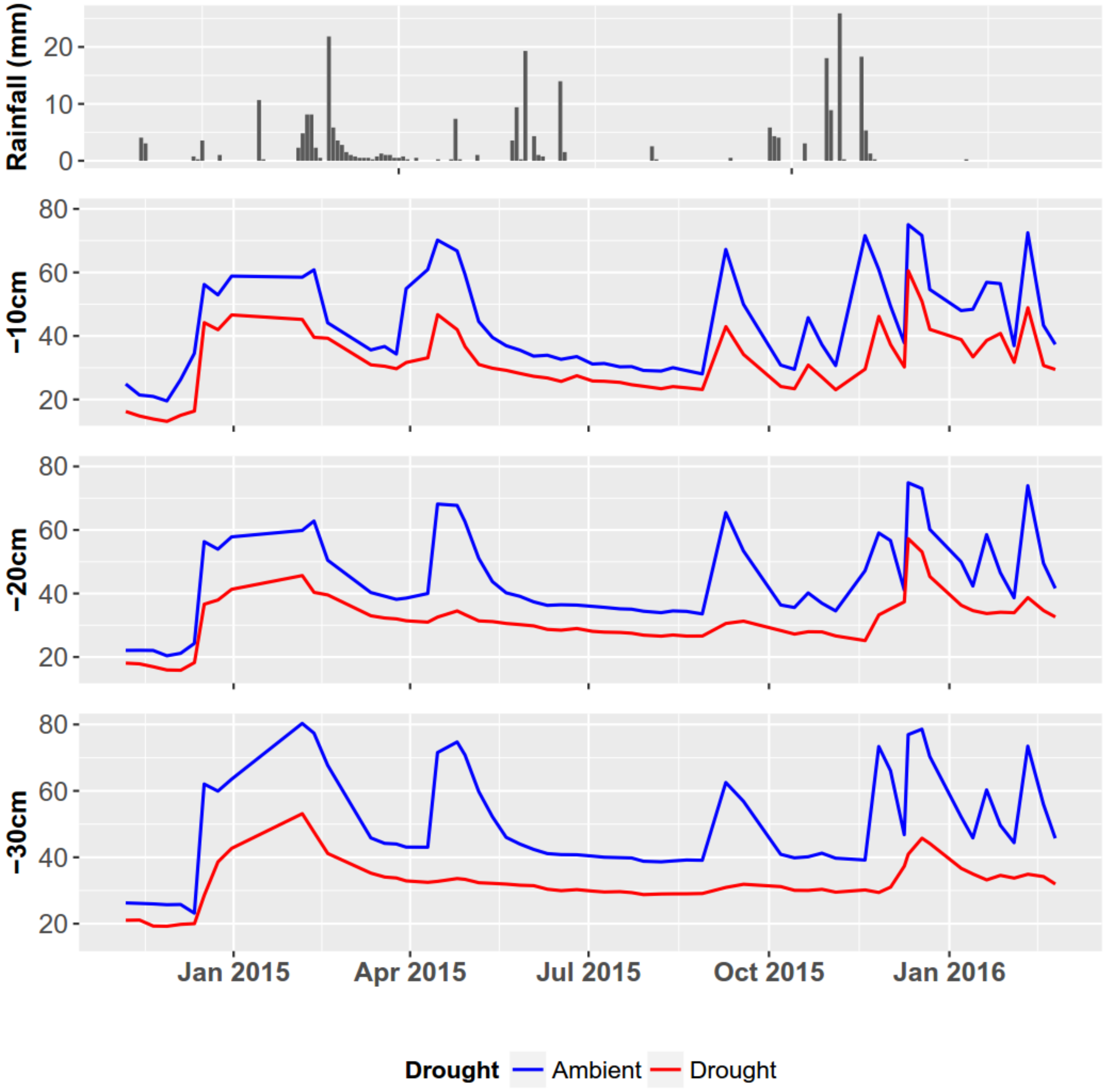

Figure 3.6: Trends in precipitation and soil moisture under drought and ambient conditions recorded at DroughtAct after installation of rainout shelters from November 2014 to March 2016.

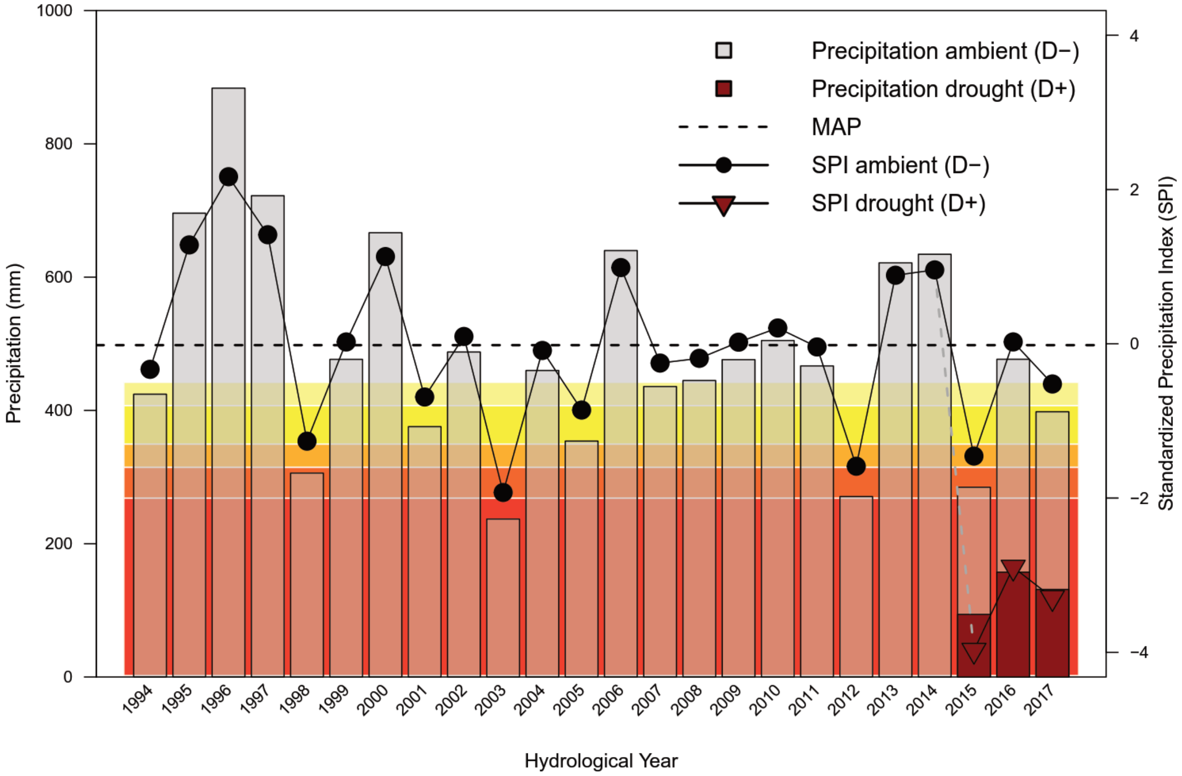

Figure 3.7: Precipitation trends for 13 hydrological years at the DroughtAct experimental site from the Syferkuil onsite weather station showing ambient precipitation, drought imposed precipitation, mean annual precipitation (MAP = 489 mm, CV = 31.8%), standardized precipitation index (SPI) for the hydrological year in ambient conditions and under drought treatment.

3.3.3 Early vegetation responses

As regards early vegetation responses, cover of live vegetation material was significantly reduced by two seasons of resting ($\chi^2 = 29.4$, $P < 0.001$) but neither drought nor the interaction of drought and resting had effects on live material (Fig. 3.8A). Standing dead material was significantly affected by resting ($\chi^2 = 42.3$, $P < 0.001$) and the interaction of drought and resting ($\chi^2 = 18.7$, $P < 0.001$). Tukey tests of the interaction indicated that dead material was lowest under ambient conditions during the first season of resting (Fig. 3.8B). In the second season of resting, standing dead material increased but was comparable to that under drought conditions in the first season of resting. Like standing dead material, the life : dead ratio was significantly affected by resting ($\chi^2 = 30.4$, $P < 0.001$) and by the interaction of drought and resting ($\chi^2 = 20.3$, $P < 0.001$, Fig. 3.8C). Tukey tests on the interaction indicated that the life : dead ratio was generally higher during the first season of rest and particularly under ambient conditions. Litter cover was not influenced by drought treatment but increased significantly on the second season of grazing exclusion (Fig. 3.8D).

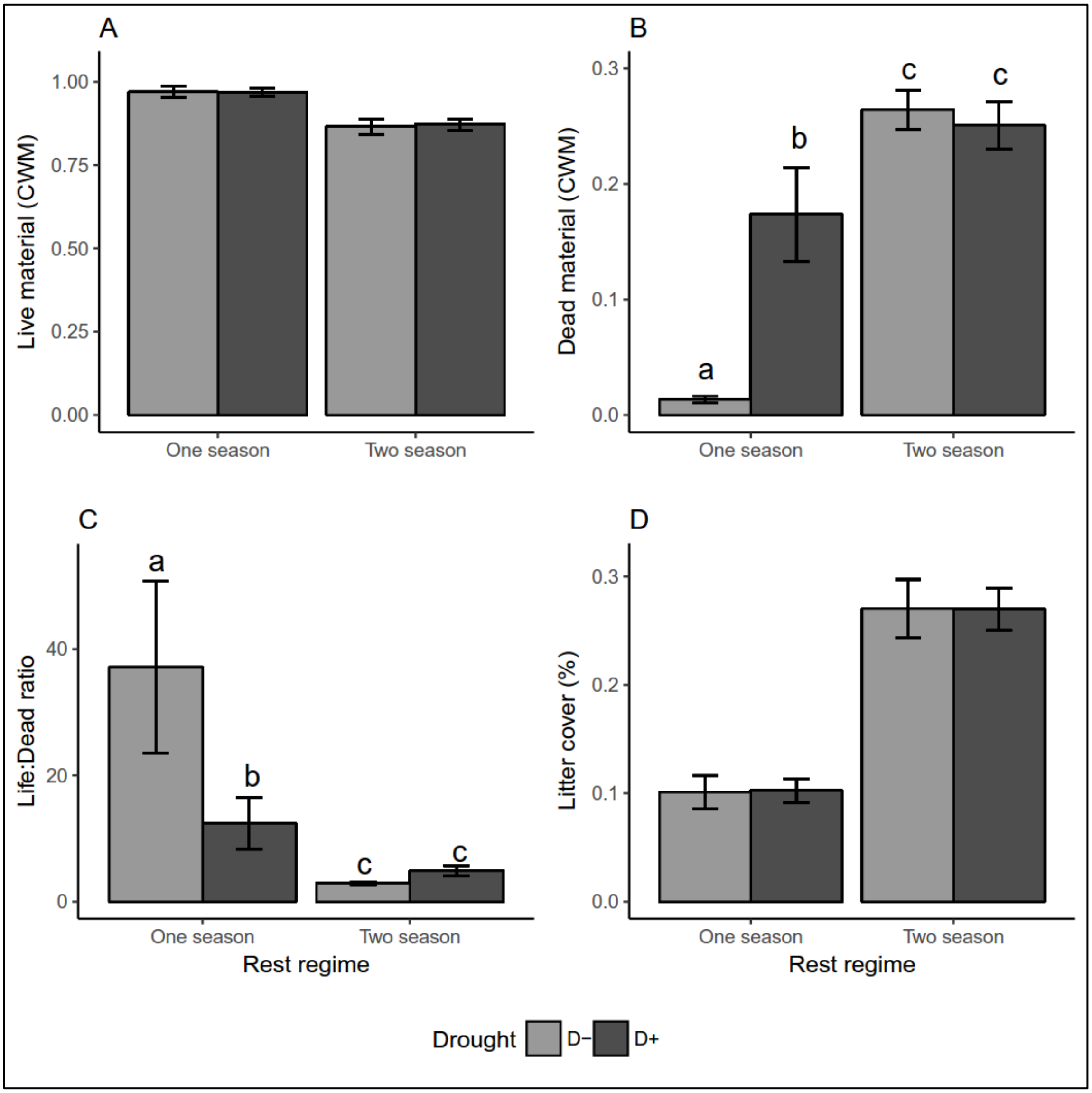

Figure 3.8: The influence of one and two season veld-resting regime on community weighted mean (CWM) live material **A**, standing dead (moribund) material **B**, life to dead ratio **C**, and litter accumulation **D** on vegetation subjected to drought (D+) and ambient rainfall conditions (D-) measured over two growing seasons 2014/15 and 2015/16 at DroughtAct experiment.

3.4 Discussion

The pre-treatment site data did not show any signs of systematic selection bias, with all vegetation and most soil parameters comparable across the experimental blocks. The few instances on which soil parameters (i.e. moisture, pH, total N and extractable Zn) differed between the blocks could be linked to the differences in maximum soil depth between the blocks. Block C was the shallowest with a hard rocky layer at depths as shallow as 22 cm (Table 3.1), possibly providing a perched groundwater layer closer to the surface which may explain the higher soil moisture and pH at the block (Miguez-Macho et al., 2008, Xu et al., 2015). However, the few observed differences in soil nutrients between the blocks could also be a result of urine and dung deposition from grazing cattle at the camp. Nevertheless, the detected variability in soil properties between the blocks is not uncommon considering the spatial scale of the experiment. But, the similarity observed in the vegetation data across the blocks suggests that the observed differences in soil parameters did not affect vegetation characteristics measured, hence it is assumed that starting conditions were relatively uniform.

The rainout shelter design had little or no artefact effects on the microhabitat while at the same time allowing free grazing by large herbivores. Thus the shelters had very minimal effects on PAR, air temperature and relative humidity. Light interception, an unavoidable artefact of field experiments involving fixed roof shelters (Fay et al., 2000, Power et al., 2016), was relatively little (13.6 %) and insignificant, consistent with other studies using similar structures for precipitation manipulation (Yahdjian and Sala, 2002, Cherwin and Knapp, 2012). Although other studies using total rainfall interception shelters have reported larger shelter effects on PAR (Fay et al., 2000, Vogel et al., 2013, Power et al., 2016), the radiation transmitted by these shelters remain within light saturation levels sufficient for photosynthesis and productivity (Turner and Knapp, 1996). Similarly, differences in minimum, maximum and relative humidity beneath and outside the shelters were all very minimal, indicating that the shelters had no effects on air temperature and humidity irrespective of time of day - particularly plausible given the height of our shelters, thus consistent (for temperature) with shelter effects documented in previous studies (Yahdjian and Sala, 2002, Cherwin and Knapp, 2012, Power et al., 2016).

With regard to grazing, shelter influences on grazing preference as measured by grazing-offtake under and outside the shelters were not detected, suggesting that vegetation under both drought and ambient conditions was equally utilized. While this indicates no shelter artefact effects, it is also consistent with theories related to aridity and grazing. According to the convergence model of aridity and grazing (Coughenour, 1985, Milchunas et al., 1988, Milchunas and Lauenroth, 1993, Quiroga et al., 2010), water stress and grazing act together to select plant traits that have higher drought and grazing resistance, where tolerance to one essentially includes tolerance to the other. For instance, Quiroga et al. (2010) found that water stress and grazing both selected for drought tolerance by means of sexual production and leaf growth, and grazing avoidance by means of lower shoot : root ratios and digestibility.

In addition, the grazing management (i.e. the stocking density and duration of grazing) at DroughtAct is particularly tailored to avoid selective grazing hence grazing selection on vegetation either under water stress or ambient conditions was not detected. But, until further information on forage quality and traits of the grazed material is known, the nonselective grazing behavior observed remains speculative. But, further vegetation characterization that include ANPP, functional traits and forage quality responses to drought and grazing treatments will be presented in subsequent publications of DroughtAct. From these surveys, the characteristics of the forage material will be determined.

As expected, the rainout shelter design successfully intercepted incoming precipitation, translating into 53%, 27% and 20% lower soil moisture under drought compared to ambient conditions at 10, 20 and 30-cm depths, respectively. This large decrease in soil moisture corresponds to the exceptional and extreme droughts imposed by the treatments in the 2014/15 and 2015/16 seasons, respectively. Temporal soil moisture trends also showed that the drought treatment reduced rain water reaching deeper soil layers as seen from the smaller peaks in soil moisture at 20 and 30-cm depths. Similar shelter effects on soil water content were reported elsewhere (Yahdjian and Sala, 2002, Cherwin and Knapp, 2012). However, the lack of grazing effects on soil moisture may be attributed to the moderate grazing pressure practiced at the farm where sufficient cover remains after a grazing event hence conserving soil moisture.

Although the area experienced a severe natural drought as a result of the El Nino in 2014/15, coinciding with implementation of the drought treatment, it is believed that, though more intense, the treatment is a valid representation of future more extreme scenarios that can be expected in our region (Knapp et al., 2008, Cherwin and Knapp, 2012, IPCC, 2014). In addition, the occurrence of above average rainfall in the year preceding the treatment implementation and below average rainfall during the treatment years provides a good opportunity to evaluate community and ecosystem response to extreme events (Alba et al., 2017, Knapp et al., 2017a). Thus the shelters served the intended purpose of intercepting rainfall and hence reducing soil moisture significantly to impose a severe drought and water stress on vegetation especially on the rooting zone. Therefore, the community and ecosystem responses to extreme drought treatments at DroughtAct are interpreted in the context of the region's long-term precipitation patterns (Alba et al., 2017) interpreted via the SPI of the hydrological year (McKee et al., 1993, Ruppert et al., 2015).

Our results on vegetation cover suggest that, even under drought conditions, the rangeland vegetation may not be rested for more than one season to avoid accumulation of standing dead material that may inhibit production of new tissue through self-shading (Zimmermann et al., 2010). Undesirable effects of self-shading on productivity of grass tufts have been reported for other savanna rangelands, where palatable perennial grasses showed the least tolerance to self-shading compared to their unpalatable counterparts and hence low productivity of the former. Thus, resting-related self-shading (Zimmermann et al., 2010) and drought-related tiller mortality (Hodgkinson and Muller, 2005) have interactive effects that ultimately result in death of tufts and thus rangeland degradation.

Apart from self-shading effects, increasing litter cover was another result of two seasons of grazing exclusion that is believed to have influenced vegetation dynamics. Depending on the amount deposited, litter influences plant community structure. For instance, increasing litter cover reduced species richness and evenness in a rough fescue grassland (Lamb, 2008), changed community composition of semi-arid grasslands (He et al., 2011) and reduced density and richness (Carson and Peterson, 1990). Whilst it had no interaction with resting, drought had additive effects on litter accumulation perhaps by slowing decomposition rates as a result of limited moisture (Aerts, 2006, Butenschoen et al., 2011). Consequently, for a veld in good condition, with a good cover of palatable perennial grasses like the DroughtAct site, one season of rest even under severe drought conditions is sufficient to prevent degradation. However, longer resting periods may be necessary in heavily degraded areas (Linstädter, 2009).

The expectations of DroughtAct go beyond conventional climate change experiments. In addition to the DroughtNet approach of realistic drought treatments (Knapp et al., 2017a), realism in global environmental change experiments was further incorporated for assessment of global change drivers in two ways; 1) For a biotic global change driver (Power et al., 2016), a real grazing treatment was factored in to the drought treatments to evaluate in combination the effects of these divers on community response. But most importantly and uniquely, 2) post-drought treatments (after two and four years of drought) were introduced to evaluate ecosystem resistance and resilience to drought, and also directly test realistic management interventions in the face of global environmental change. In this regard, DroughtAct is currently on its fourth treatment year (as per IDE recommendations) and is expected to continue into the fifth year in order to capture both the in-drought and post-drought treatment responses.

Furthermore, in addition to the vegetation metrics presented in this chapter, routine surveys on plant phenology, plant functional traits, species composition, material decomposition and plant population dynamics in response to our treatment combinations are also carried out at DroughtAct. All these vegetation surveys are carried out according to globally accepted methods and protocols. Thus, all these aspects of DroughtAct makes it a prototype for a new generation of global change experiments, providing options to add real grazing and post drought treatments to existing global change experiments. In addition, DroughtAct's factorial design has the potential to generate a much greater understanding of the interactive impacts of drivers, and thus contributing to solving the current 'experimental imbalance' in global change research (Flombaum et al., 2017).

Going forward, establishment of similar parallel long-term experiments in other environments (Alba et al., 2017), with ecosystem-specific treatments to assess differential sensitivity across multiple ecosystems (Knapp et al., 2017a) are encouraged. Thus, DroughtAct sampling protocols will be made available, particularly for real grazing treatments and post drought management interventions for researchers interested in adding realism to conventional global change experiments for ease of comparisons.

3.5 Conclusions

It was demonstrated that the rainout shelters had little or no artefact influence on the microhabitat. The drought treatment served the intended purpose of reducing precipitation and hence soil moisture without influencing the microhabitat and the grazers' behavior. The selected early vegetation response data indicated that, for semi-arid rangelands under moderate grazing and characterized by good cover of palatable perennial grasses, rest regimes longer than one season will degrade the veld irrespective of climatic condition. The increase in litter and moribund material at the expense of live material by the second season of rest clearly suggests that one season rest is sufficient to recover the veld even under severe drought conditions in these areas.

While the set up established DroughtAct as a prototype for a new generation of global change experiments, the selected early results on soil properties, grazing offtake and behavior and grazing exclusion effects on vegetation, further provided an overview of ecosystem responses that can be measured using our experimental approach. Thus, this chapter will help other researchers interested in establishing realistic, multi-factorial global change experiments to allow for cross-site comparisons and hence contribute to solving the current 'experimental imbalance' in global change research. The next chapter looks at large-scale grazing management (continuous grazing versus short duration grazing and resting) effects on perennial grasses and woody vegetation from two cases studies in cattle ranches of Botswana.

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CHAPTER 4: The Role of Cattle Grazing Management on Perennial Grass and Woody Vegetation cover in Semiarid Rangelands: Insights from Two Case Studies in the Botswana Kalahari

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The Role of Cattle Grazing Management on Perennial Grass and Woody Vegetation Cover in Semiarid Rangelands: Insights From Two Case Studies in the Botswana Kalahari

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Abstract

The long-term effects of continuous and rotational grazing on grass and tree dynamics were assessed on adjacent ranches in the semiarid Kalahari of western Botswana. Rotationally grazed ranches had higher grass cover with more perennial grass species, higher grazing value (and capacity), and higher long-term stocking rates than their continuously grazed neighbors. Tree cover tended to be higher on continuously grazed ranches, suggesting that long-term continuous grazing reduced grass production and favored establishment of woody vegetation. Improvement in semiarid rangeland health and production is unlikely to be achieved simply by reducing stocking rates; uniform grazing and growing season recovery periods are essential. These and other case studies suggest that benefits of grazing strategies likely depend on scale and adaptive management. Future research should be at larger spatial and temporal scales.

Keywords: Continuous grazing, grazing capacity, grazing value, rotational grazing, stocking rate

4.1 Introduction

Grazing management practices are broadly defined as reoccurring periods of grazing, resting and deferment of pastures (Heitschmidt et al., 1991). For simplicity grazing systems are categorized into two broad types; continuous grazing (CG) which involves season-long grazing of the entire management unit and rotational grazing (RG) which involves moving a herd through multiple pastures within a matrix of paddocks in varying phases of recovery from grazing (Teague et al., 2004). Rotational grazing practices are meant to increase grass and animal production, promote more uniform grazing and maintain favorable grass species composition (Heitschmidt et al., 1991, Teague et al., 2013).

Inappropriate grazing practices may result in undesirable vegetation change in rangelands including an increase in woody vegetation and a decrease in perennial grass species leading to reduced carrying capacity (Milton et al., 1994). Productive perennial grasses exert strong competitive effects on woody species, thereby greatly retarding their growth (Riginos, 2009). The effects of reduced competition by the grass layer may be exacerbated by reduced fire intensity and frequency, leading to unimpeded woody plant establishment and growth.

Rangeland researchers and managers worldwide continue to debate the efficiency of continuous and rotational grazing practice in maintaining rangeland vegetation and livestock production (Teague et al., 2013). Meta-analyses of grazing experimental data have found little or no advantages of RG over CG, with stocking rate rather than grazing system consistently emerging as the most important management factor determining range condition and animal performance (Briske et al., 2008). However, Teague et al. (2013) identified problems associated with small-scale grazing experiments and provided ranch-scale evidence for the benefits of adaptive RG over CG. These authors argued that results from grazing experiments that have relatively small spatial and temporal scales bear little resemblance to the effect of long-term ranch-scale management.

That notwithstanding, small scale experimental research has demonstrated that defoliation of grasses via clipping or grazing reduces their productivity in subsequent years (Turner et al., 1993), indicating that grasses need periods of non-grazing during the growing season to allow them to recover nutrients lost to grazing. Without sufficient time for recovery, repeatedly grazed perennial grasses will eventually be replaced by ungrazed (less palatable) neighbors and annual grasses (Turner et al., 1993, Milchunas and Lauenroth 1993), especially on infertile sandy soils, where recovery of nutrients lost after grazing is more difficult than on fertile soils. These shifts in species composition to plants of lower grazing value, and in dominant life form from perennial to annual, may result in a decline in carrying capacity (Milton et al., 1994).

In western and north western Botswana, cattle ranching is the main land use practice and an important economic and livelihood strategy in the rangelands (Masike and Urich, 2008). Grazing practices in this area vary from communal areas without a defined system of grazing to commercial ranching in fenced private farms with distinct grazing practices (Moleele et al., 2002). While there is uncertainty over the efficacy of RG compared with CG (Teague et al., 2004, Briske et al., 2008), both systems (at different levels of intensity) are widely used by ranchers. However, signs of undesirable rangeland conditions have been reported in both commercial cattle ranches and communal areas in this area (Kgosikoma et al., 2012a). In an attempt to monitor and improve rangeland condition in these areas, local government authorities set stocking rates guided by carrying capacities according to the amended grazing policy on agricultural development of 1991 (GoB, 1991).

To acquire more ecological understanding of the dynamics of grasses and woody vegetation between the grazing practices, we conducted two studies on two pairs of adjacent ranches, where in each pair, one practiced RG and the other CG, in all cases for many (12 to 21) years in western and north western Botswana. Our objective was to determine the effect of RG vs CG on perennial grass cover, composition, biomass and woody vegetation cover. We hypothesized that persistence of perennial grasses and woody vegetation cover would differ with ranches subjected to RG showing significantly higher persistence of perennial grasses and lower woody vegetation cover. We expected to provide insights that would advise policy and ranchers on grazing management strategies in semiarid rangelands particularly on sandy infertile soils.

4.2 Materials and methods

4.2.1 Study site

We selected two pairs of adjacent ranches, where in each pair, one practiced RG and the other CG practices, at two separate sites in the Kalahari ecosystem of Botswana. Both Gantsi and Ngamiland district have a semi-arid climate with cold dry winters and hot wet summers with a mean annual precipitation of 430 mm and 460 mm, respectively (Bhalotra, 1987). Soils at both study sites are deep Kalahari sands with low nutrients and organic matter content (Skarpe and Bergstrom, 1986). One site was at Farm 122 and Farm 120-121 in Gantsi District in western Botswana (21°53’42.17”S and 21°49’53.58”E). The other site was at Farm 12 and Farm 11 of the Hainaveld ranches in Ngamiland District in north western Botswana (20°26’30.05”S and 23°25’39.9”E).

Gantsi is characterized by open shrub savanna with scattered trees and perennial tufted grasses, dominated by silky bushman grass (*Stipagrostis uniplumis)* and common finger grass (*Digitaria eriantha)*. Vegetation of the Hainaveld ranches is dominated by raisin bush (*Grewia* spp.) and silver terminalia (*Terminalia sericea*) woodland with grass layer characterized by *Digitaria eriantha* and love grasses (*Eragrostis* spp.) (Privette et al., 2004). The annual recommended stocking rates for Gantsi and Hainaveld as determined by the Department of Animal Health and production during the time of survey were 19 ha Large Stock Unit^{-1} (LSU, where a LSU is equivalent to 450 kg bovine live mass) and 17 ha LSU^{-1}, respectively. However, the recommended stocking rates vary from year to year depending on rainfall and vegetation conditions.

4.2.2 Management Strategies on the Ranches

While some of the ranches we assessed kept detailed records, we acknowledge that information on past management strategies on some of the ranches beyond 15 years was in most cases not available and as a result we depended on anecdotal information by the ranch owners.

4.2.2.1 Gantsi – RG

Farm 120-121 (18800 ha) is a private commercial cattle ranch with a network of fences dividing it into 64 paddocks with eight water points. The water points are located in the center of a wagon wheel pattern of radiating fences of paddocks. It has an advanced intensive grazing system that involves moving multiple herds of cattle (main herd >2000) to graze each paddock for a week and then allowing the grazed paddock to recover for at least 3 months. The system is more than just a simple rotation of cattle between paddocks as it also involves pasture assessments in individual paddocks prior to grazing. There were 3554 mature cattle on the ranch during the study period and this equated to 5.3 ha LSU$^{–1}$, which was more than three times the recommended stocking rate of the region (19 ha LSU$^{–1}$). The stocking rate and the system of grazing had been maintained for 21 years since 1990 (Dudley Barnes – the ranch owner, personal communication, October 2011).

4.2.2.2 Gantsi – CG

Farm 122 (15000 ha) is also a privately owned commercial cattle ranch in Gantsi adjacent to Farm 120-121. The ranch is not divided into any paddocks and it has only one water point located at the north-western corner. It has been continuously grazed at low stocking densities for at least 15 years since 1996. Information from the Gantsi veterinary department (although it has gaps on some years) indicates that cattle numbers have fluctuated from 745 (20.1 ha LSU^{-1}) in 1996 to 582 (25.8 ha LSU^{-1}) in 2004. In 2005 ownership of the ranch changed but grazing management remained unchanged until 2011 (time of this survey). During this time, there were 400 head of cattle in the ranch (37.5 ha LSU$^{–1}$), which is about half the recommended stocking rate (19 ha LSU$^{–1}$).

4.2.2.3 Hainaveld - RG

Farm 12 (5000 ha) is a commercial cattle ranch at Hainaveld practicing a less intensive system of RG. The ranch is divided into six paddocks where cattle spend two months in each paddock. Three paddocks (half of the ranch) are always grazed in the wet season and the other three in the dry season. Paddocks that are grazed in the dry season get a full wet season recovery period. Each of the paddocks grazed in the wet season gets at least three months of recovery time either early or late in the growing season depending on when it was grazed, and remain ungrazed throughout the dry season. During the time of survey, there were 450 head of cattle at ca. 11.1 ha LSU^{-1} (Sekeletu pers. comm. June 2015). The average stocking density over a 12 year period since 2002 leading up to the study was 13 ha LSU^{-1}.

4.2.2.4 Hainaveld - CG

Farm 11 ranch (5000ha) practices CG at ca. 22 ha LSU^{-1}. The ranch does not have a defined grazing practice and one herd of cattle graze the entire ranch without paddocks throughout the season. The grazing practice has been maintained for more than 15 years since 1999. Records from the animal health department indicate that the ranch has been stocked at an average of 20 ha LSU^{-1} over a period of 15 years (1999 – 2014).

4.2.3 Vegetation Assessment Methods

A fenceline contrast approach was used to survey vegetation differences between the ranches at both sites. However, different vegetation assessment methods were used at the two sites. For grazing value (palatability) and life form (perennial or annual) of grasses, the classification of van Oudtshoorn was used. Both research and management levels of confidence associated with statistical significance of differences on vegetation dynamics between grazing management types for decision-making purposes were considered.

The Gantsi contrast was carried out in February 2012 along the eastern boundary of Farm 120-121, practicing rotational grazing (RG) and Farm 122, practicing continuous grazing (CG). Grass assessments were conducted in pairs of adjacent transects such that each pair consisted of one transect in the RG and the other on the CG ranch. A total of 13 pairs of transects were surveyed along a 7-km fenceline. Transects were 55 m long and were located at 500-m intervals perpendicular to the fenceline (Fig. 4.1). To avoid edge effects of the fence, sampling was started 20 m from the fenceline and a kilometer away from the water point on the CG ranch to avoid piosphere effects. A 100-m measuring tape was used to maintain transect lengths and a 1-m^2 quadrat was placed five times every 5 m along each transect for grass assessments.

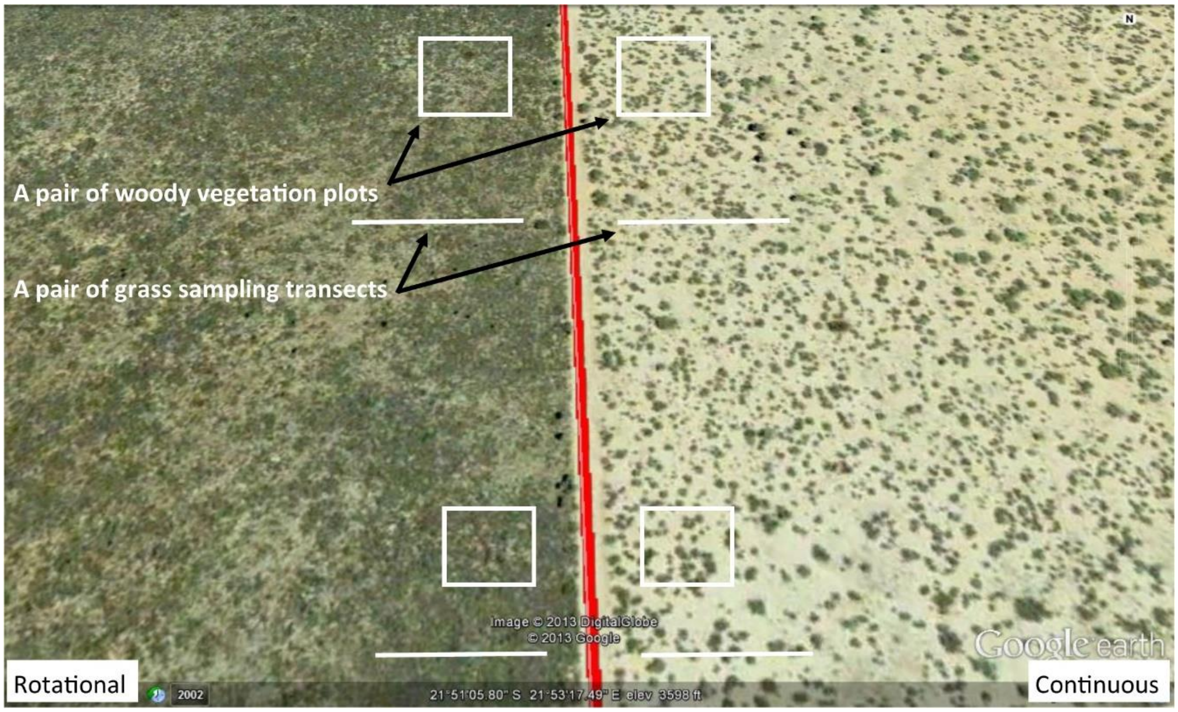

Figure 4.1: A Google Earth image showing pairs of woody vegetation assessment plots and grass sampling transects drawn along a fenceline (red line) dividing a rotationally grazed and a

continuously grazed ranch of Gantsi district in western Botswana. Plots in each pair measure 40 x 40 m and pairs are 500-m apart.

All grass species (excluding forbs) rooted within the 1-m^2 quadrat were identified and percentage canopy cover of each species was visually estimated. To determine aboveground grass biomass (current year and previous years dead material) plants were clipped using 0.25-m^2 quadrat within the bigger 1-m^2 quadrat. Clipped material was dried in a forced-air oven at 60°C for 48 hours and weighed.

Woody vegetation cover at Gantsi was sampled using remotely sensed images of the ranches from Google Earth. Ten pairs of 40 x 40 m plots, 500-m apart, positioned 20 m perpendicular to the fenceline, were drawn on the images, where each pair had one plot in the RG and another plot in the CG ranch. The images were cropped to plot sizes, saved as JPEG files and processed on ImageJ (image processing software: Pascal, 2013) to determine areas of tree canopies in each plot. The scale on ImageJ to was set to 40 (known length of plot) and units to meters in order to spatially calibrate the images. Tree canopies were visible on the images as dark green color hence only the dark green portions of the image were measured. The calculated canopy areas were used to represent woody vegetation cover.

At Hainaveld, grass and woody vegetation cover assessments were conducted in June 2015 using the variable quadrat method with adjustments (Coetzee and Gertenbach, 1977), along the shared fenceline of Farm 12 under RG and Farm 11 under CG. Quadrat sizes were started at a minimum of 10 x 10 m (5 m each side of the intersection of the ropes), followed by 20 x 20, 30 x 30, 40 x 50 x 50 and ended at 60 x

60 m. Paired plots were laid (one plot in RG and the other in CG) systematically at 500-m intervals along the fenceline with the center of each plot at 50-m away from the fenceline. At both sites, the classification of van Oudtshoorn to identify grasses to species level and classify in to life forms and grazing value was used (van Oudtshoorn, 1999).

Paired samples t-test was used to determine statistical significance of the differences in total grass cover, biomass and woody vegetation cover between the ranches at all sites. Normality was tested by running a Shapiro-Wilk test and non-parametric Wilcoxon’s matched-pairs test was used when data did not satisfy the assumptions of normality. The 90% ($P < 0.10$) and 95% ($P < 0.05$) confidence level in statistical significance testing to represent basis of decision-making by management and research, respectively, was used. Species diversity indices where determined by calculating a Shannon diversity index (H').

4.3 Results of Grazing Management

Refer to Table 4.1 for the response of woody vegetation cover and grass dynamics to grazing management. Total grass cover and perennial grass cover at Gantsi were higher on the RG while annual grass cover was higher on the CG ranch. Similarly, at Hainaveld, total grass cover and perennial grass cover were higher on RG than CG ranch, while annual grass cover did not differ between the ranches. Aboveground biomass (current year and previous years dead) and species diversity did not differ between the RG and CG but species richness was higher on the CG ranch in Gantsi. However, at Hainaveld, the RG ranch had a higher grass species diversity than the CG ranch with the same number of species.

Table 4.1: Cover by life form, grass biomass, species richness and diversity on adjacent ranches practicing continuous or rotational grazing, in two districts of western Botswana.

Site	**Parameter**	**Grazing management**		***t* statistic**	***P*-value**
		Rotational	Continuous		
Gantsi	Woody plants cover (%)	35.9±6.61	43.3±11.24	2.45	0.081†
	Annual grass cover (%)	5.3±2.10	11.5±3.02	2.62	*
	Perennial grass cover (%)	49.0±5.81	27.1±4.54	3.29	**
	Total grass cover (%)	51.8±16.90	35±11.62	2.53	*
	Standing biomass (g^{-2})^{i}	41.7±5.12	32.7±6.60	1.24	0.231
	No. Species	4.77±0.33	5.7±0.21	2.65	**
	Shannon diversity index (*H*')	1.73	1.58	0.16	0.880
Hainaveld	Woody plants cover (%)	37.9±6.45	54.0±11.9	1.92	0.061†
	Annual grass cover (%)	4.08±2.01	2.69±1.23	1.15	0.351
	Perennial grass cover (%)	27.5±5.62	7.28±1.21	2.50	*
	Total grass cover (%)	33.9±6.12	8.83±1.30	3.32	**
	No. Species	1	1	-	-
	Shannon diversity index (*H*')	1.29	0.5	3.22	**

† < 0.10, * < 0.05, ** < 0.01, *** < 0.001
Data are mean per plot and standard error. The *t* and *P* values are from a paired samples t-test.
Standing biomass was not measured at Hainaveld ranches.

At the higher confidence level normally used for research (95%), woody vegetation differences between the ranches were not significant but at the lower and acceptable confidence level associated with management decision-making (90%), there were more woody species on CG ranches at both sites. The aerial view of the Gantsi fenceline contrast also shows larger tree sizes on the CG and more grass cover on the RG grazed ranch (Fig. 4. 2).

Figure 4.2: An aerial photograph visualizing the difference in vegetation cover on adjacent ranches practicing continuous and rotational grazing in Gantsi district in western Botswana. (Photo Credits, Dudley Barnes).

Refer to Table 4.2 and Figure 4.3 for the effects of grazing management on individual grass species of different life forms and grazing value. Cover of high grazing value species was higher on RG than CG ranches at both sites. While cover of medium grazing value species was not different between RG and CG in Gantsi, it was higher on the RG than CG at Hainaveld. Black-footed grass (*Brachiaria nigropedata*), a high grazing value species, and silky bushman grass (*Stipagrostis uniplumis*), a medium grazing value species, dominated the RG and CG ranch, respectively. Cover of annuals, Natal redtop

(*Melinis repens)* and crab finger grass (*Digitaria sanguinalis),* also a low grazing value species, were higher on the CG than RG ranch at Gantsi. Common finger grass (*Digitaria eriantha)*and sand quick (*Schmidtia pappophoroides*), all perennial species of high grazing value, and medium grazing value broad curly leaf (*Eragrostis rigidior*) were higher on the RG than the CG ranch at Hainaveld.

Table 4.2: Cover of grass species of different grazing value on adjacent ranches grazed rotationally or continuously, in two districts of western Botswana

Site	Species	Grazing value[ii]	Life form[iii]	Cover (%)		z statistic	*P* value
				Rotational	Continuous		
Gantsi	*Aristida congesta*	1	A	0	0.03±0.02	-1.41	0.16
	Aristida meridionalis	1	P	0	1.95±1.19	-1.60	0.13
	Brachiaria nigropedata	3	P	25.4±5.98	1.22±0.72	-2.94	**
	Digitaria eriantha	3	P	1.64±1.03	2.61±1.52	-1.47	0.24
	Digitaria sanguinalis	1	A	1.93±1.23	4.62±1.43	-2.04	0.21
	Eragrostis lehmanniana	2	P	5.00±1.35	3.72±1.27	-0.71	0.40
	Eragrostis pallens	1	P	1.38±1.09	0.61±0.61	-0.45	0.50
	Eragrostis rigidior	2	P	4.60±4.37	0.31±0.31	-0.54	3.48
	Melinis repens	2	A	2.21±0.91	5.44±1.51	-2.12	*
	Schmidtia pappophoroides	3	P	2.33±1.53	0.34±0.31	-1.21	0.24
	Stipagrostis uniplumis	2	P	6.32±1.70	17.8±4.89	-2.55	*
	Urochloa trichopus	3	A	1.12±0.79	1.53±0.80	-0.97	0.71
Hainaveld	*Aristida congesta*	1	A	0.24±0.18	0.29±0.18	-0.48	0.65
	Dactyloctenium aegyptium	2	A	0.60±0.60	0.08±0.03	-0.69	0.40

Digitaria eriantha	3	P	11.69±3.76	1.35±0.55	-2.25	*
Eragrostis rigidior	2	P	11.39±1.87	4.71±1.33	-2.38	*
Melinis repens	2	A	1.38±0.38	0.91±0.31	-0.70	0.40
Pogonarthria fleckii	1	A	2.01±1.73	0.06±0.03	-1.12	0.28
Schmidtia pappophoroides	3	P	3.86±0.94	0.35±0.14	-2.15	*
Stipagrostis uniplumis	2	P	0.60±0.28	0.86±0.35	-0.63	0.58
Tragus racemosa	1	A	0.05±0.03	0.01±0.01	-1.03	0.19
Urochloa trichopus	3	A	1.80±1.39	1.34±0.46	-0.51	0.67

* < 0.05, ** < 0.01, *** < 0.001
Data are mean per plot and standard error. The *z* and *P* values are from a Wilcoxon's matched-pairs test. Grazing value is consistent with van Outshoorn (1999) where; 1 = low grazing value, 2 = average grazing value, 3 = high grazing value. Life form; A = annual, P = perennial.

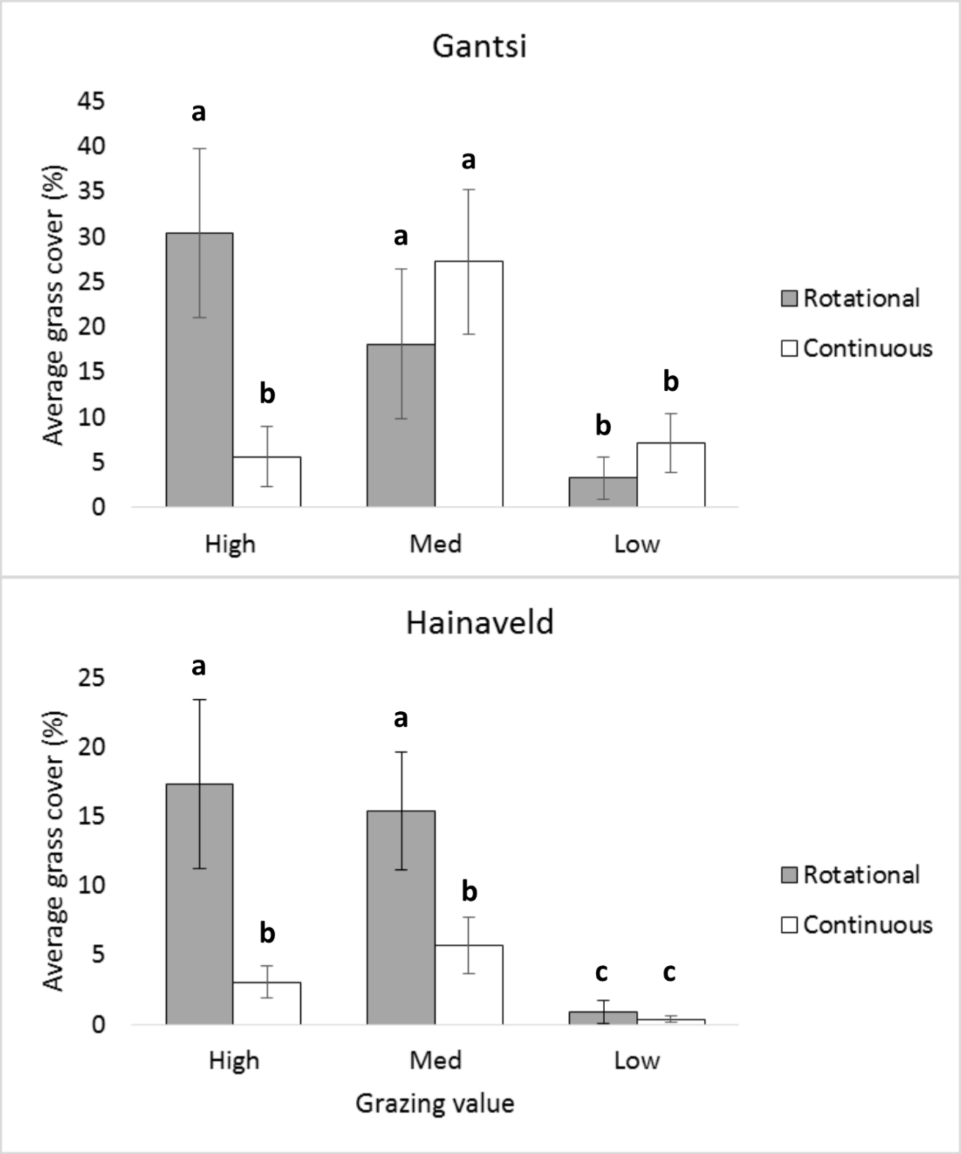

Figure 4.3: Mean cover (± SE) of grass species of different grazing values on adjacent ranches practicing continuous and rotational grazing in two districts of the Kalahari in western Botswana. Different letters indicate significant differences (Wilcoxon's matched pairs test; $P < 0.05$).

4.4 Implications for Grazing Management

In our two case studies, grazing practice changed grass cover and proportion of grass life forms and grazing value. The higher total and palatable perennial grass cover on RG compared to CG ranches, despite the high stocking rates in RG ranches, suggest the importance of recovery periods for grasses to recover nutrients lost to grazing in infertile soils and the benefits of high stocking rates to promote even grazing distribution. At high stocking rates, selectivity is reduced as grazing impacts are evenly distributed over the paddocks, hence both palatable and unpalatable species experience similar grazing levels (Teague et al., 2013). However, under similar levels of defoliation, palatable grasses are more tolerant of defoliation than unpalatable grasses (Teague et al., 2013). While the use of multi-paddock grazing with high stocking rates for short durations, such as the Gantsi RG improves forage resources, it may also be labor and cost intensive. Nonetheless, grazing management that uses few paddocks such as the Hainaveld RG may also improve forage resources with less intensive management.

As seen on CG ranches, low stocking rates are not sufficient to promote perennial grass establishment. This is because under CG at low stocking rates, cattle selectively graze the palatable species which are not afforded adequate recovery, hence promoting uneven grazing distribution (Teague et al., 2013, Steffens et al., 2013, Norton et al., 2013). While continuous grazing at appropriate stocking rates appears to be sustainable in fertile environments (Briske et al., 2008), on the infertile Kalahari sands, plant nutrient loss under grazing has much greater consequences for perennial grass persistence than in ecosystems with more fertile soils where nutrients are more easily replaced after removal in grazed tissue Noy-Meir, 1973). The grazed grasses in these infertile soils would be unable to adequately recover key growth-limiting nutrients such as nitrogen when continuously selectively grazed under a CG strategy. Therefore, while stocking rates form an integral part of grazing management, they must be applied together with management that supports uniform grazing and adequate recovery of the available forage to reduce overgrazing.

In addition to cover, grass species composition changed in response to grazing management. At Hainaveld, while species richness did not differ between grazing management, the diversity was higher on RG perhaps because of the abundance of few dominant species. Similarly, the higher number of species on the CG than the RG ranch at Gantsi suggests an increase of tail-end (minor unabundant) species that result from diminishing dominant species that are continuously selectively grazed (Walker et al., 1999). Under appropriate grazing management that promotes uniform grazing and adequate recovery of grazed plants, minor species are out-competed by the dominants and make up a relatively small proportion of cover (Walker et al., 1999). On the other hand, grass biomass (not measured at Hainaveld) including moribund material was not different between grazing management perhaps as a result of an accumulation of moribund material from the abundant silky bushman grass that was apparent under CG.

Apart from changes in grass dynamics, grazing management also changed woody vegetation cover. At the 90% confidence level, woody vegetation cover was higher on CG than RG suggesting that grazing management may have affected woody cover. Indeed, this would be expected seeing that continuous grazing has reduced grass cover, which may exert strong competitive effects on trees (Riginos, 2009). The high stocking density on RG would strongly suppress establishment of trees as animals are forced to eat and also trample on saplings.

4.5 Conclusions

To conclude, this chapter provides a useful insight that grazing management that promotes even grazing distribution at appropriate stocking rates, and adequate recovery periods of grazed paddocks in the growing season, is important for maintaining the cover of palatable perennial grasses in semiarid rangelands. In sandy infertile soils, such grazing management is critical to allow recovery of nutrients lost to grazing and rebuilding of root biomass, which is likely more rapidly achieved in fertile soils. RG ranches had higher grass cover with more perennial grass species of higher grazing value (and capacity), at higher long-term stocking rates than their CG neighbors. Tree cover tended to be higher on CG ranches, suggesting that long-term continuous grazing reduced grass production and favored establishment of woody vegetation. Thus, ranch managers and policy makers should not rely on changing stocking rates as a sole means of improving rangeland productivity and condition, especially in regions with sandy soils.

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CHAPTER 5: The Role of Herbivore Impact and Subsequent Timing and Extent of Recovery Periods in Rangelands

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Role of Herbivore Impact and Subsequent Timing and Extent of Recovery Periods in Rangelands[☆,☆☆]

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Abstract

The productivity and stability of cattle production on rangelands depends upon the maintenance of a dense and productive perennial-grass-dominated resource base, which is contingent upon appropriate grazing and recovery periods. The effect of simulated trampling, dung inputs, frequency of defoliation in the previous growing season (grazing history) and timing of recovery periods on various grassland functional responses was investigated in two experiments in western and northwest Botswana. A field-based clipping experiment at the individual tuft scale demonstrated that perennial grasses are most productive when rested for a full growing season, but that productivity of the highly palatable soft leaved *Brachiaria nigropedata* Ficalho & Hiern. decreases exponentially with increasing clipping frequency in the previous season (a lagged effect of grazing history). This species was also more productive in the next season when rested during the early than late growing season. The less palatable needle leaved *Stipagrostis uniplumis* Licht. ex Roem. & Schult. was less resistant to defoliation than *Brachiaria nigropedata* and decreased equally at each clipping frequency regardless of season. A second field-based experiment at the plot scale demonstrated that a full-season recovery period increased tuft densities while its combination with dung increased cover. The effects of hoof trampling on sandy nutrient-poor grasslands appear to be less significant compared to grasslands on fertile soils. Thus, optimal-livestock-management strategies should aim to promote season-long grazing of both palatable and unpalatable species to disadvantage the less grazing tolerant unpalatable species, and full growing season recovery periods to ensure optimal recovery and future productivity.

Key words: Defoliation frequency, palatable grass, recovery period, sandy nutrient-poor soils, trampling

5.1 Introduction

The effect of grazing on above ground net primary productivity (ANPP) has been the subject of much debate for a long time (Westoby, 1985, McNaughton, 1985, 1993, Belsky et al., 1993, Dyer et al., 1993, Painter and Belsky, 1993, Hiernaux and Turner, 1996, Knapp et al., 2012). While several studies worldwide demonstrated that large herbivore grazing stimulates grassland productivity, otherwise referred to as overcompensation (McNaughton, 1979, 1984, Noy-Meiyer et al., 1989, Turner et al., 1993, Frank et al., 1998), others argued that evidence supporting the concept of overcompensation in grazed swards is inadequate (Westoby, 1985, Painter and Belsky, 1993, Hiernaux and Turner, 1996, Knapp et al., 2012).

However, the nature and effect of grazing is not mono-dimensional or linear but varies according to the degree of selectivity by grazers (Morris et al., 1992, Fynn, 2012), the intensity of grazing (Briske et al., 2008), the nature and evolutionary history of the grasses (tufted versus creeping; long-term history of herbivory) (Milchunas and Lauenroth, 1993, Fynn, 2012) and the spatial and temporal scales at which grazing occurs (Frank et al., 1998, Fynn, 2012). Thus the effects of grazing on grassland productivity cannot be reliably predicted without knowing specific details of the spatial and temporal scale at which grazing occurs and the types of grasses being grazed. For example, moderate levels of grazing generally stimulate grassland productivity in large scale migratory ecosystems where the effects of grazing are concentrated and transient

(McNaughton, 1985, Frank et al., 1998) but reduces productivity (undercompensation) in non-migratory ecosystems where grazing is often non seasonal and continuous (Milchunas and Lauenroth, 1993, Knapp et al., 2012). Nevertheless, at very high levels, grazing generally reduces productivity irrespective of its spatial and temporal scale across landscapes (McNaughton, 1979, 1985, Turner et al., 1993, Heirnaux and Turner, 1996, Owen-Smith, 2002).

A strong theoretical and empirical foundation that underlies current scientific understanding of competitive outcomes among plants under differential nutrient loss rates has been established (e.g. Tilman, 1988, Berendse et al., 1992, Tomlinson and O'Connor, 2004). Heavy continuous grazing runs down nutrient stores in the plant through removal of nutrients and carbohydrates in grazed tissue (Berendse et al., 1992), but to a lesser degree carbohydrate stores because grasses are unable to store much carbohydrate (Danckwerts, 1993). This compromises the plants nutrient economy resulting in reduced tillering and productivity (Berendse et al., 1992, Tomlinson and O'Connor, 2004), which is exacerbated by poor root development and inability of plants to access deep-layer soil moisture and growth limiting nutrients (Hodgkinson and Bass-Becking, 1977). Thus, several studies across three continents have demonstrated that grazing in the previous growing season strongly reduced productivity of grasses in the next growing season (Turner et al., 1993, Ash and McIvor, 1998, Knapp et al., 1999, Kirkman 2002). Consequently, long term selective grazing of palatable perennial grasses results in their ultimate death or competitive exclusion by unpalatable species that do not get grazed much (Morris et al., 1992, Anderson and Briske, 1995, Dube and Gwarazimba, 2000, Fynn, 2012).

Most rotational grazing strategies involve a period of grazing of paddocks followed by a period of recovery, with one to several iterations over the growing season. However, the effectiveness of these within season recovery periods for restoring effective root systems, nutrient stores and vigor will likely depend upon the availability of soil moisture and nutrients for growth and storage in crowns and roots, which can be recycled to aerial growth in the next season. The fact that nutrients are not mineralized evenly over the growing season but rather in pulsed events (Fierer and Schimel, 2002), the bulk of which occurs during spring (Scholes and Sanchez, 1990, Higgins et al., 2015), suggests that recovery periods during times of good rainfall, especially during the early-growing-season, will be more effective for grasses than during drier periods or during the late growing season. Much attention has been given to the effect of defoliation frequency and intensity on grass productivity and community composition (e.g. Danckwerts and Nel, 1989, Turner et al., 1993, Anderson and Briske, 1995, Hiernaux and Turner, 1996, Kirkman, 2002) but very little attention has been given to the timing of recovery periods in relation to rainfall and nutrient mineralization and this important aspect needs attention.

Apart from the direct effects of grazing, grazing may also have indirect effects on grasslands, such as through its associated trampling effects and dung and urine inputs, which improve forage quality and grassland productivity by increasing rates of nutrient cycling and removing light inhibiting litter (Knapp and Seastedt, 1986) as well as promoting seed burial and establishment (McNaughton, 1983, 1985, Georgiadis and McNaughton, 1990, Frank et al., 1998). Apart from anecdotal evidence (McNaughton 1983) and some experimental studies (e.g. Wilson and Tilman, 2002), little attention has been given to the importance of the effects of physical disturbances of the soil surface by trampling in determining community composition through effects on grass seedling recruitment and aerial litter removal. Thus grazing at the right spatial and temporal scale may provide beneficial ecosystem engineering effects that positively influence ecosystem processes and functioning (Jones et al., 1994), which may then lead to feedback effects on plant composition and productivity (McNaughton et al., 1988).

This chapter aimed to determine how the frequency of defoliation (simulated grazing by clipping) and timing of recovery periods affects perennial grass productivity and survival as well as how the indirect effects of grazing via trampling and dung affected grass biomass and cover. Four hypotheses were postulated: 1) Increasing grazing intensity will reduce grass productivity in subsequent seasons, 2) Timing of recovery periods will influence productivity in subsequent seasons, 3) Dung inputs will increase grass and forb biomass and cover, and 4) Clipping, trampling and dung will have an interactive influence on cover and biomass in grassland communities.

5.2 Materials and methods

5.2.1 Study site

The study was conducted in two separate but complementary experiments in Botswana, examining how clipping frequency affects grass productivity and survival. One experiment was conducted at Barnes Oasis ranch located approximately 24 km south-east of Gantsi Township at 21°53’42.17”S and 21°49’53.58”E. The other study site complementing the Gantsi sites was located on the Okavango Research Institute (ORI) campus situated 15 km northwest of Maun at 19°54’19.29’’S and 23°31’51.6’’E. Maun and Gantsi fall within the Kalahari ecosystem characterized by deep Kalahari sands, hence have slightly variable but comparable conditions.

Climate in the Gantsi area is arid to semi-arid with mean monthly winter minimum temperatures of 5°C and summer highs of 33°C (Bhalotra, 1987). Mean annual precipitation (MAP) is 430 mm (Botswana Meteorological Services) with the greater proportion occurring between October and April (Thomas, 2002). About 60% of the rainfall occurs between January and March. Rainfall amount and distribution are variable resulting in recurring droughts (Cole and Brown, 1976, Bhalotra, 1987). Although total annual rainfall at Barnes Oasis ranch decreased during the study period (2011/12 to 2012/13), the area received more rain during the early season (December) in 2011 and during the late season (January and February) in 2013 (Fig. 5.1A). Maun has a relatively similar climate to Gantsi with a slightly higher MAP of 460 mm (Botswana Meteorological Services). The majority of the rainfall occurs between November and March (Ellery et al. 1990; Ellery et al. 1991). However, there was a decrease in annual rainfall during the study period from 2010 to 2013 (Fig. 5.1B). Temperatures in Maun are relatively high throughout the year with a mean monthly low of 7°C in winter and a high of 34°C in summer (Botswana Meteorological Services).

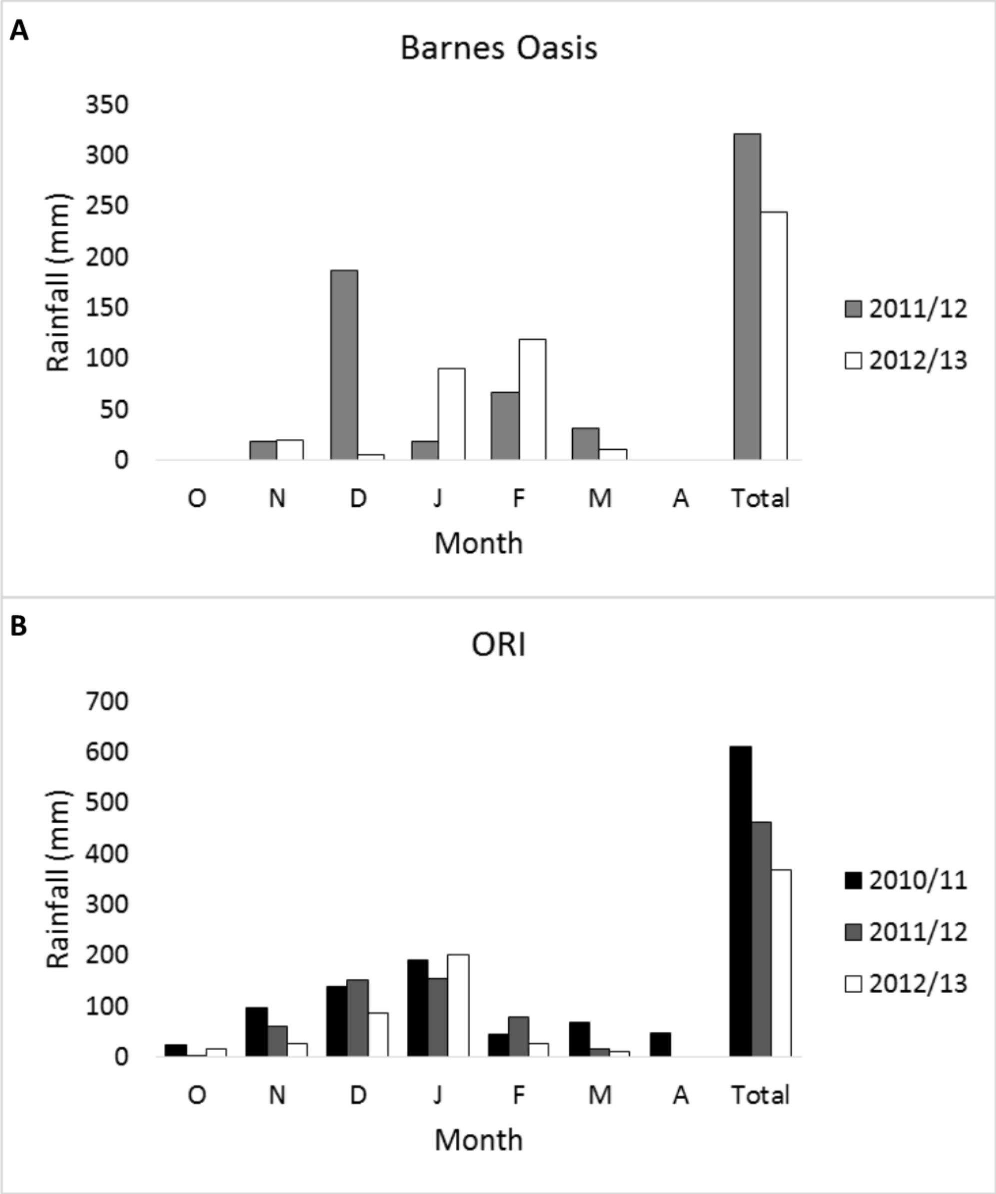

Figure 5.1: Monthly and annual precipitation data for the 2011/2012 and 2012/2013 growing seasons at the Barnes Oasis ranch in western Botswana (A) and for the 2010/2011 – 2012/2013 seasons at the ORI experiment in northwestern Botswana (B). Source: Barnes Oasis and ORI records.

The soils in Gantsi and Maun are predominantly Kalahari sands, which typically consist of over 95% sand (Thomas and Shaw, 1991) with rare bedrock exposures (Cole and Brown, 1976). The sands are mostly deep, structureless and are very low in N, P and organic matter (Skarpe and Bergstrom, 1986, Dougill et al., 1998). Vegetation of the Gantsi area is characterized by open shrub savanna with scattered trees and perennial tufted grasses (Skarpe, 1986), where *Terminalia sericea* Burch. ex DC. is a common woody species. The grass layer is dominated by *Stipagrostis uniplumis* and *Digitaria eriantha* Steud. (Cole and Brown, 1976, van Oudtshoorn, 1999). Vegetation around Maun is characterized by *Colophospermum mopane* Kirk ex Benth. woodland on alluvial soils and with patches of *Terminalia sericea* woodland on deep Kalahari sands (Privette et al., 2004), as in the Gantsi region. Nomenclature for all plant names is according to Germishuizen et al. (2006).

5.2.2 Data Collection

5.2.2.1 Barnes Oasis Ranch Experiment

Two experimental sites within 2 km of each other (and hence with similar growing conditions), one dominated by *S. uniplumis* and the other by *B. nigropedata* were identified on Barnes Oasis ranch. These C4 grass species were selected because they are the most dominant species on the ranch (Mudongo, 2014) and are good examples of a hard needle-leaved, less palatable and a soft-leaved, highly palatable species, respectively (van Oudtshoorn, 1999). Each experimental site was fenced off with a wire-strand fence with additional fine-mesh chicken wire to protect grasses within the experiment from grazing. The chicken mesh wire was also buried about 20 cm below ground level to keep hares out. The experiment was set up as a random complete block design with 10 blocked replicate tufts of the dominant species at that site. Five clipping treatments (Table 5.1) were randomly allocated to five tufts of each grass species per block. Tufts that were not less than 5 cm in basal diameter were selected. Neighboring plants were never close enough to cause shading of experimental tufts and hence were not clipped. Each clipping treatment was denoted by colour-coded steel rods, which were used to mark the selected tufts. While clipping was used to simulate grazing by cattle, we realize that cattle rarely graze tufts to low levels so the clipping represented very intense grazing. All marked tufts were first clipped down (about 5 cm above the ground) in the dry season (September 2011) to remove senescent material before the growing season for accurate measure of above-ground productivity.

Table 5.1: Design of clipping treatments for Brachiaria nigropedata and Stipagrostis uniplumis tufts during the 2011/2012 and 2012/2013 growing season at Barnes Oasis Ranch in western Botswana.

Treatment	No. clips	Code	2011/2012				2012/2013			
			Dec	Jan	Feb	Mar	Dec	Jan	Feb	Mar
No rest	4	NR	X	X	X	X	X	X	X	X
Early season rest	2	ESR			X	X			X	X
Late season rest	2	LSR	X	X			X	X		
Cut once only	1	COF			X				X	
Full season rest	0	FSR					X	X	X	X

The crosses indicate months when tufts were clipped. Clipping was done once at the end of the month.

Clipping treatments were done in two growing seasons commencing from December 2011 to March 2012 for the first season and December 2012 to March 2013 for the second season (Table 5.1). Tufts were clipped at 5 cm above the ground with the use of clippers. Prior to the first clipping event, the circumference of each tuft was measured with a flexible measuring tape. This would then be used to calculate the initial tuft area, with productivity being expressed per unit tuft area to standardize comparisons. After each clip all material was collected in brown paper bags, oven-dried at 60°C for 48 hours and weighed for biomass. From the treatments that were clipped, productivity was taken as means of the summed monthly clips in the season.

Productivity in the full season rest (FSR) treatments was measured in the second year by sorting plant material into previous season’s dead (oxidized) and current season (green and brown) (e.g. Knapp et al., 2002). Productivity of each surviving tuft was calculated as biomass per initial tuft area to standardize for different tuft sizes. In the first season of the Barnes Oasis ranch experiment, cattle twice managed to break through the fence of the *B. nigropedata* experiment and some experimental tufts were moderately grazed. Owing to the high replication of treatments, however, (10 blocks) potential confounding effects of these two grazing events do not seem to have over ridden clipping treatment effects, which constituted a far more severe defoliation.

5.2.2.2 ORI Clipping/Dung/Trample Experiment

Another clipping experiment that had been running in a homogeneous area of grassland at the ORI from November 2009 to February 2013 was used to complement the experiment at Barnes Oasis Ranch. Experimental treatments were applied in the wet seasons of 2009–2010, 2010–2011 and 2011–2012 with assessments of treatment effects being done in 2013. Grazing was simulated by clipping. A three factor random complete block design of 16 treatments replicated seven times to make 112 plots was used in the experiment (four clipping x two soil trampling x two dung addition, Table 5.2). Plots measured 1.5 x 1.5 m, with 1 m wide walkways between rows of plots and 0.75 m spacing between plots in a row. The clipping treatments were; 1) clipped at the end of December and March every year (C1), 2) clipped at the end of December and March every alternate year (C2), 3) continuously clipped at the end of November, December, January, February and March every year (CF) (November not clipped if rains came late) and 4) unclipped control (Cont). Soil trampling (T) and dung addition (D) treatments were applied (Table 5.2).

In 2010, soil trampling was simulated by chipping the soil surface with an axe but was changed to stamping and breaking the soil with a 6-cm diameter wooden pole (considered similar to the impact of cattle hooves) at the end of March and October in 2010 but in 2011 and 2012 it was only carried out in October (Table 5.2). Dung inputs involved addition of 200 g of crushed cattle dung per plot where the amount was calculated from studies of dung deposition in East Africa (David Augustine, unpublished data). An amount equivalent to six months of deposition was chosen to represent the time migratory grazers would spend in a seasonal range. Dung inputs were applied just prior to the soil trampling treatment in October to allow for the effect of trampling on dung incorporation in the soil.

Table 5.2: Design for the clipping, trampling and dung treatments during the 2010, 2011 and 2012 seasons at the ORI experiment in northwestern Botswana.

Treatment	Code	2010						2011						2012					
		J	F	M	O	N	D	J	F	M	O	N	D	J	F	M	O	N	D
Clipped twice every year	C1			X			X			X			X			X			X
Clipped twice every alternate year	C2			X			X									X			X
Clipped five times every year	CF	X	X	X		X	X	X	X	X		X	X	X	X	X		X	X
Control (unclipped)	Cont																		X
Dung addition	D				X						X						X		
Trampling	T			X	X						X						X		

The crosses indicate the months when treatments were applied.

In February 2013 the aerial cover of each grass species and forbs, bare ground, and litter cover, as well as above-ground biomass were measured in each plot. Tuft density was recorded in each plot by counting the number of grass tufts in a 0.5 x 0.5 m quadrat placed in the center of each plot (to avoid edge effects). Above-ground biomass was determined by harvesting all plants in the 1 m^2 quadrat and separating into forbs and grass. The aerial cover of each grass species in a plot was determined by giving a visual percentage estimate of its cover within the plot. All harvested plant components (forbs, current-years grass and previous-years dead were oven-dried at 60°C for 48 hours and weighed. Rainfall data for the period of the study was obtained from the Barnes oasis and ORI onsite weather stations.

5.2.3 Statistical Analysis

For both experiments, significance of difference between treatments was obtained by carrying out linear mixed-effects model (using treatments as fixed effects and block as a random effect) with analysis of variance (ANOVA) and Tukey HSD multiple comparisons in R. At the Barnes Oasis experiment, initial tuft size was used as a covariate in the ANOVA. We tested effect of clipping frequency in the first season (0, 1, 2 or 4 clips) on second season productivity of *B. nigropedata* and *S. uniplumis* by performing a nonlinear and linear regression, respectively on a sample size of 50 individuals of each species ($n = 50$). The control in this analysis (0 clips in first season) was the full season rest treatment (Table 5.1) where previous-years dead material that had accumulated in the full rest of the first season, and was clipped in the December clip of the second season, was discarded as we were only interested in second season's growth. Previous year's dead material (grey in colour) could easily be distinguished from second-seasons growth, which was either live (green) or senesced (brown). After the first clip (December) only second season’s growth remained for the January, February and March clips. Thus none of our productivity assessments were based on using previous-years dead, where some material may be lost through decomposition, which ensured all treatments in the analysis were comparable (second seasons growth only). Normality of the data was tested by Shapiro-Wilk test whereas homogeneity of variance was checked by examining residuals plots. A binary logistic regression analysis was conducted to predict the odds of survival of tufts using treatment and tuft area as predictors. The test predicts the probability that the dependent variable is either a success or failure using a Wald statistic to assess the significance of coefficients. Residuals were observed and data violating ANOVA assumptions (tuft density and standing biomass) were log-transformed.

5.3 Results

5.3.1 Barnes Oasis Ranch Experiment

Second season productivity for both *B. nigropedata* and *S. uniplumis* decreased with increasing first season clipping frequency, but the decline for *S. uniplumis* was much more abrupt and dramatic at any clipping frequency (Fig. 5.2). The full season rest (FSR) treatment resulted in the highest productivity for both *B. nigropedata* and *S. uniplumis* in the second season (Table 5.3). A single cut (COF) treatment reduced productivity of *B. nigropedata* by more than 50% in comparison to the FSR treatment (Table 5.3). For *B. nigropedata*, the early season rest (ESR) treatment resulted in greater productivity than the late season rest (LSR) treatment despite both treatments having the same clipping frequency (Table 5.3).

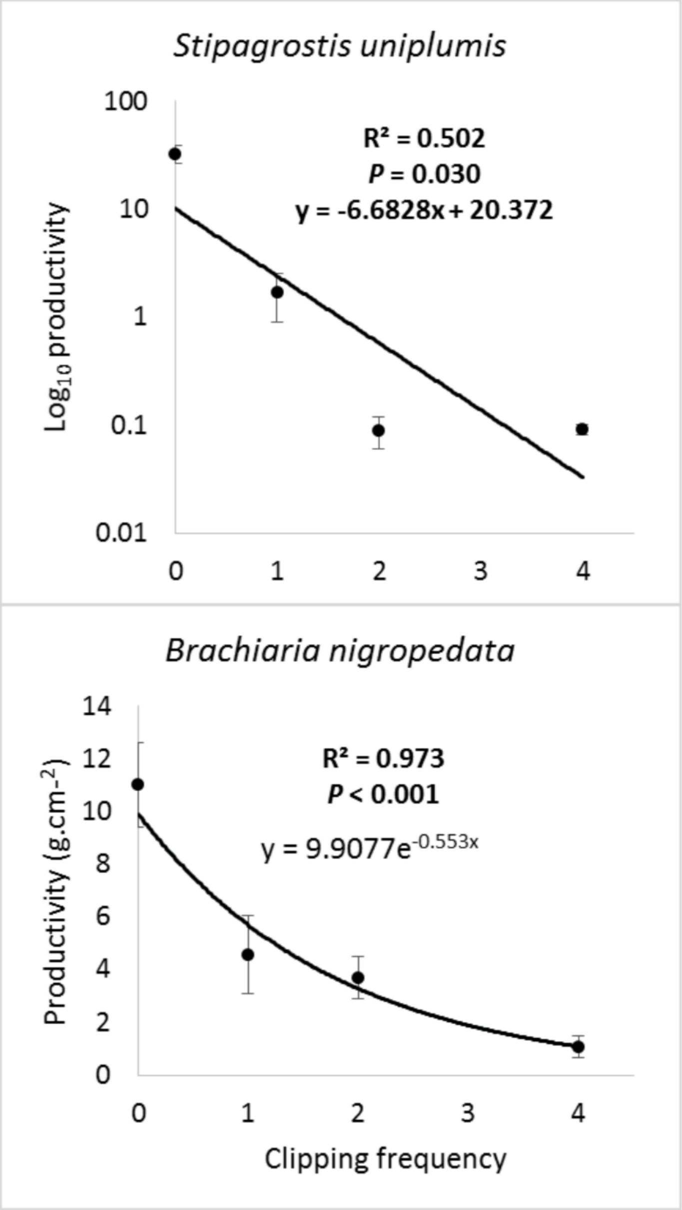

Figure 5.2: Response of Brachiaria nigropedata and Stipagrostis uniplumis second season productivity to first season clipping frequency during 2011/2012 and 2012/2013 growing seasons at Barnes Oasis ranch in western Botswana. The *P* values (significant values with $P < 0.05$) and R^2 are from a non-linear and linear (*B. nigropedata* and *S. uniplumis*, respectively) regression of 50 individuals ($n = 50$) of each species.

Table 5.3: Mean (±SE) second year productivity of *Brachiaria nigropedata* and *Stipagrostis uniplumis* under different first season clipping treatments during the 2011/2012 and 2012/2013 growing season at the Barnes Oasis ranch in western Botswana.

		Brachiaria nigropedata	*Stipagrostis uniplumis*
Treatment	No. Clips	Productivity (g•cm^{-2})	Productivity (g•cm^{-2})
No rest	4	1.08a ± 0.41	1.98a ± 0.39
Early season rest	2	5.29b ± 1.29	0
Late season rest	2	2.15a ± 0.69	0
Cut once only	1	4.57b ± 1.46	1.72a ± 0.81
Full season rest	0	11.0c ± 1.61	32.8b ± 6.42

Means with a different letter in a column indicate significant differences based on multiple comparison of Tukey's post hoc test.

While clipping treatment did not influence tuft mortality in *B. nigropedata*, the no rest (NR) and COF treatments made a significant contribution to *S. uniplumis* tuft mortality prediction (Table 5.4). There was an 11% and 44% chance of survival of *S. uniplumis* tufts under the NR and COF treatments, respectively (Table 5.4). Tuft area did not influence mortality in either species ($P > 0.05$, Table 5.4).

Table 5.4: Prediction of survival and death of tufts of Brachiaria nigropedata and Stipagrostis uniplumis using clipping treatment and tuft area as predictors from the Barnes Oasis experiment in western Botswana.

	Brachiaria nigropedata						*Stipagrostis uniplumis*					
Predictor	Died	Survived	Wald	EXP(B)	Odds ratio	*P*	Died	Survived	Wald	EXP(B)	Odds ratio	*P*
No rest	4	6	0.92	0.38	0.68	0.341	9	1	8.7	0.01	0.11	**
Early season rest	1	9	0.38	2.25	0.92	0.543	5	5	3.2	0.08	0.49	*
Late season rest	0	10	0	NA	0.99	1.000	0	10	0	NA	0.99	1.000
Cut once only	1	9	0.38	2.25	0.92	0.543	6	4	4.4	0.06	0.44	*
Full season rest	0	10	0	NA	0.99	1.000	0	10	0	NA	0.99	1.000
Tuft area	7	53	2.76	1.02	0.80	0.100	21	39	1.88	1.01	0.70	0.172

* < 0.05, ** < 0.01, *** < 0.001

NA – not applicable.

The odds ratios and associated *P* values are from a binary logistics regression.

5.3.2 ORI Clipping/Dung/Trample Experiment

Clipping treatment and its interactions with dung and trampling had significant effects on grass cover and tuft density (*P* < 0.05, Table 5.5). Dung alone did not influence herbaceous vegetation variables (*P* > 0.05, Table 5.5) whereas trampling influenced forb cover (*P* < 0.05, Table 5.5). Cover of forbs increased from 21.6 ± 3.2 in control treatments to 28.4 ± 2.96% in trampled treatments.

Table 5.5: The main effects of clipping treatment, dung addition, trampling and their interactions on grass cover, standing biomass, tuft density and forb cover measured during February 2013 at the ORI experiment in northwestern Botswana.

Source		Grass cover		Standing grass biomass		Tuft density		Forb cover	
	Df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Clipping treatment	3	1.63	0.211	3.13	*	13.5	***	0.14	0.812
Dung	1	0.58	0.463	0.01	0.943	0.45	0.511	0.01	0.980
Trampling	1	1.87	0.200	0.02	0.888	0.01	0.932	5.44	*
Clip x Dung	3	3.69	*	2.44	0.090	8.92	***	0.27	0.853
Clip x Trampling	3	5.49	*	3.40	*	8.23	***	0.81	0.500
Dung x Trampling	1	1.62	0.230	1.57	0.233	0.03	0.864	2.77	0.131
Clip x Dung x Trampling	3	9.65	***	0.47	0.700	5.23	*	0.98	0.420

* < 0.05, ** < 0.01, *** < 0.001
The degrees of freedom (Df), *F* and *P* values are from an ANOVA of mixed effects model.

Grass cover was highest (> 70%) in plots clipped in alternate years (receiving a year-long recovery period) and receiving dung (C2D) but was comparable to plots clipped every year combined with trampling and dung additions (C1DT) and those plots clipped in alternate years with dung and trampling (C2DT and C2 each at 61.7%, Table 5.6).

Table 5.6: Mean (±SE) grass cover and tuft density in response to clipping and its interactions with dung and trampling measured during February 2013 at the ORI experiment in northwestern Botswana.

Treatment	Grass Cover (%)	Tuft density*(no•m^{-2})
Clipped twice every year (C1)	55.8c ± 1.05	17.0c ± 0.24
Clipped twice every alternate year (C2)	61.7dc ± 1.16	18.9d ± 0.33
Clipped five times every year (CF)	53.1bc ± 1.00	16.3bc ± 0.29
Control (Cont)	39.3a ± 0.74	14.8a ± 0.18
C1 x Dung (D)	55.9c ± 1.05	16.9c ± 0.25
C2 x D	72.7d ± 1.37	18.9d ± 0.35
CF x D	51.9bc ± 0.98	16.1b ± 0.30
Cont x D	47.1ab ± 0.88	14.7a ± 0.22
Cont x Trample (T)	27.6a ± 0.60	15.1a ± 0.25
C1 x D x T	63.0dc ± 1.19	18.0c ± 0.44
C2 x D x T	61.7dc ± 1.16	19.1d ± 0.36
CF x D x T	56.0c ± 1.06	16.3bc ± 0.29
Cont x D x T	26.7a ± 0.64	15.5ab ± 0.30

Means with a different letter in a column indicate significant differences ($P < 0.05$) based on multiple comparison of Tukey's post hoc test. Only those treatments with significant effects are shown.

* Values were log transformed for statistical analysis

Tuft density was highest in plots clipped in alternate years (C2) and did not differ when dung (C2D) or a combination of dung and trampling (C2DT) was added (Table 5.6). Aboveground grass biomass was highest in control plots and lowest in plots clipped and trampled every year (C1T) (Table 5.7). However, clipping twice every year (C1) and clipping twice every alternate year (C2) yielded comparable grass biomass to the control treatments (Table 5.7).

Table 5.7: Mean (±SE) standing grass biomass in response to clipping and its interactions with trampling measured during February 2013 at the ORI experiment in northwestern Botswana.

Treatment	Standing biomass*(g•m^{-2})
Clipped twice every year (C1)	71.7abc ± 1.66
Clipped twice every alternate year (C2)	72.5bc ± 1.78
Clipped five times every year (CF)	71.0ab ± 1.82
Control	76.5c ± 1.33
C1 x Trample (T)	67.4a ± 1.48
C2 x T	69.7ab ± 1.52
CF x T	70.6ab ± 1.92
Control x T	77.4c ± 1.42

Means with a different letter in a column indicate significant differences (P < 0.05) based on multiple comparison of Tukey's post hoc test. Only those treatments with significant effects are shown.
* Values were log transformed for statistical analysis

5.4 Discussion

Several key results from the tuft clipping experiment on Barnes Oasis Ranch provide important insights and contributions to the debate on grazing effects on compensatory growth in rangelands (e.g. McNaughton, 1985, Westoby, 1985, Painter and Belsky, 1993, Knapp et al., 2012). The experiment demonstrated that productivity of *B. nigropedata* and *S. uniplumis* decreased exponentially and linearly, respectively with increasing clipping frequency, such that second season productivity was greater for tufts not clipped in the first season (FSR) than tufts clipped in the first season. This is perhaps because by the second growing season the tufts clipped over the first growing season (NR, ESR, LSR and COF) had incurred reoccurring loss of photosynthetic tissue. Loss of photosynthetic tissue results in losses of photosynthetic-derived carbon and growth-limiting nutrients, which would have been recycled and used for regrowth in the next season (Berendse et al., 1992, Danckwerts, 1993, Tomlinson and O'Connor, 2004). In addition, frequent and intense grazing may strongly reduce both root biomass and root depth in grasses and sedges (Archer and Tieszen, 1983, Danckwerts and Nel, 1989, Snyman, 2009), which will likely negatively impact nutrient storage and moisture and nutrient uptake for regrowth in the next season. The clipping height (~5 cm) represented severe defoliation. Thus these results demonstrate a negative lagged effect of grazing/clipping history on current season's grassland productivity.

Almost identical results to our experiment were obtained in a clipping experiment in tallgrass prairie, which showed that *Schizachyrium scoparium* Michx. increasingly undercompensated in the second and third growing seasons of clipping (Turner et al., 1993). Relative growth rates of *Andropogon gerardii* Vitman. were much greater for plants rested in the previous year compared with those grazed in the previous year (Knapp et al., 1999). Similarly, sour veldt grasses grazed in the previous growing season were much less productive in the next season than grasses rested during the previous season (Kirkman, 2002), as was the case in Australian grasslands (Ash and McIvor, 1998). Thus, although the current experimental design does not allow examination of overcompensation directly, the results suggest that overcompensation will likely only be observed in tufted perennial grasses (not lawn grasses, which are more resilient under grazing owing to lower loss rates) that have had sufficiently long recovery periods after grazing in the previous growing season to enable full recovery of nutrients lost to grazing and development of deep and strong root systems, thereby enabling vigorous regrowth after grazing in the next growing season (reducing lagged effects of grazing history). Under compensation as a result of grazing history induced lagged effects on productivity was clearly demonstrated by Turner et al. (1993).

Another important result was that *B. nigropedata* showed a seasonal effect of clipping frequency such that tufts rested early in the first growing season, such as in the ESR and COF treatments, were more productive in the second season than tufts rested late (LSR). This is despite the lower rainfall during the early months (December / January) than later months (February / March) of the 2012/13 growing season. A possible reason for this is that the late growing season is not favourable for grasses to recover nutrients lost to grazing, where peak mineralization may occur in the early growing season (Higgins et al., 2015). This is also linked to the observations that mineralization rates are much higher after rewetting of dry soils (Scholes and Sanchez, 1990, Fierer and Schimel, 2002), where soils are driest at the start of the early growing season after a long dry season in African savannas. By contrast with *B. nigropedata*, *S. uniplumis* was reduced by each clipping frequency to a similar level irrespective of season, suggesting that *S. uniplumis* is intolerant to severe defoliation at any frequency regardless of season.

While soil moisture may also limit growth in semi-arid environments, C4 grasses have an increased water use efficiency that allows them to survive under dry conditions (Edwards et al., 2010) suggesting that early season nutrient fixation and soil moisture conservation is critical in dry nutrient poor environments. This is a key and novel result that links grass productivity under clipping to the timing of rest during the growing season, which has not been demonstrated in previous studies particularly in sandy dystrophic soils.

It is suggested that N economy in grasses provides a unifying explanation of the observed grazing history effects and timing of resting/grazing on the next growing seasons productivity because both of these factors likely affect N uptake and storage (grazing removes N, while early season resting falls in the period of peak N mineralization), but this will require further investigation. For example, dry season grazing, when grasses are dormant and have translocated N to below ground stores, has much less negative effect on productivity in the next season compared with wet season grazing, where grasses would lose more N to grazing (Ash and McIvor, 1998). Similarly, grassland productivity can be linked to as far back as the previous four years rainfall events (Wiegand et al., 2004), which control mineralization pulses in soils (Scholes and Sanchez, 1990, Fierer and Schimel, 2002, Higgins et al., 2015).

The other key finding of the clipping experiment was that the palatable *B. nigropedata* was much more tolerant of clipping than the less palatable *S. uniplumis* as observed in clipping experiments comparing palatable and unpalatable species in North America (Anderson and Briske, 1995) and South Africa (Morris and Tainton, 1993). More preferred palatable grasses such as *B. nigropedata*, may be more tolerant of clipping than tough-leaved grasses such as *S. uniplumis*, but they are often replaced by these less preferred grasses under poor grazing management practices (Anderson and Briske, 1995, Morris et al., 1992). The palatable grasses are selectively eaten and over grazed, which as we demonstrated leads to declining productivity and ultimately replacement by less preferred species (Anderson and Briske, 1995, Morris et al., 1992). However, grasses that are adapted to a lack of disturbance in the form of grazing or fire have developed tolerance traits such as slow growth rates and shade tolerance to enable them to withstand reduced light levels and increased litter (MacDougall and Turkington, 2004, Fynn et al., 2011), but are less tolerant of clipping/grazing (Morris and Tainton, 1993).

The similarity of the results of the current study with several others on grazing history (Turner et al., 1993, Ash and McIvor, 1998, Knapp et al., 1999) and life history (Morris and Tainton, 1993, Anderson and Briske, 1995) effects on grassland productivity, despite regional and inter-continental separation and despite different grass species dominants, demonstrates that grazing history and life history effects are key general factors that need to be accounted for in understanding grassland productivity responses to grazing. Thus, when taking into account (1) the length of recovery after clipping/grazing (short-term grazing history), (2) the evolutionary history (grazing tolerance) and (3) the life history (palatable, soft leaved vs. unpalatable, needle leaved) of the dominant grass, the compensatory response of grasslands (over vs. undercompensation) under grazing becomes a robust and predictable concept. These results support hypotheses 1 and 2.

In accordance with the findings that season-long resting (alternate year clipping) increased grass productivity, at the ORI experiment it was demonstrated that alternate year clipping (C2) increased tuft densities irrespective of dung addition and trampling, whereas grass cover increased when dung was added (Table 5.5 and 5.6). While soil trampling has been found to increase seedling establishment (Wilson and Tilman, 2002) and hence high seedling densities (McNaughton 1983), this was not the case in the current study. A possible explanation is that the ORI study was conducted in sand veld environments where the effects of hoof trampling may be less pronounced than on hard veld environments.

Although no attention was paid to the soil type in terms of its inherent pattern of nutrient availability, the response is interpreted to have taken place in poor sands on which the rates of regrowth are accordingly expected to be slow – grasses on more fertile soils may have been less susceptible to mortality under clipping than on these sandy soils but it is expected that productivity responses to clipping history would have been the same (e.g. Turner et al., 1993, Kirkman, 2002).

5.5 Conclusions

The results of this study confirmed that a full growing season recovery period is far superior to partial resting within the growing season, as noted elsewhere by Kirkman and Moore (1995), Zacharias (1995) and Briske et al. (2011). The observation that even one cut during the growing season reduced productivity in the next growing season by half relative to a full growing season recovery suggests that partial recovery periods (early or late growing season recovery periods) are not optimal in semi-arid, nutrient poor rangelands but rather that a full growing season recovery period is the best management strategy in these rangelands.

Most rotational grazing systems worldwide include several grazing and recovery periods within each paddock over the growing season. Our data suggests that rotational resting (deferred resting) where some paddocks are grazed and others rested over the entire growing season (e.g. Kirkman and Moore, 1995) is a superior approach to grazing management. However, this may be relative to plant productivity of C4 bunch grasses and limited to the environmental conditions characterizing sandy nutrient-poor rangelands, although other studies on fertile soils and under high rainfall have drawn the same conclusions (Zacharias, 1995). Our observations that less palatable, needle leaved grasses were less tolerant of clipping than palatable soft leaved grasses suggests that managers can aim to reduce the abundance of less palatable grasses by use of non-selective grazing techniques, which encourage grazing of both palatable and unpalatable species (e.g. season-long grazing after fire to maintain unpalatable grasses in a short, higher-quality state).

5.6 References

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CHAPTER 6: General Conclusion

6.1 Introduction

The studies of this thesis were set out to explore ecosystem functioning and service provision in grazed semi-arid rangelands of southern Africa against the background of ever increasing levels of global change, and ultimately aimed to suggest viable management options and adaptation strategies. The major motivation were the predicted changes in the climate (i.e. reduced precipitation and increased frequency and intensity of droughts) and the livestock grazing system for these marginal areas, as well as the lack of adaptive capacity in the latter. From a purely scientific perspective, our limited knowledge on joint effects of drought and grazing, and hence a lack of science-based adaptation strategies to cope with increasing intensities and frequencies of drought, were an additional motivation (Chapter 1). The theoretical and empirical literature on individual and combined effects of drought and grazing in semi-arid rangelands, particularly in the context of Africa, remain largely inconclusive, posing several questions on these ecosystems' resilience and resistance to these effects (Chapter 2). Thus the study sought to answer these three questions:

1. How can the knowledge gaps in drought and grazing (combined) studies be overcome in these ecosystems?
2. How does ranch-scale grazing management influence herbaceous and woody vegetation dynamics?
3. How does herbivore impact and recovery periods influence rangeland dynamics in climatically variable semi-arid ecosystems?

In order to address the above questions and hence the problem statement, this synthesis is structured as follows:

First, I systematically discuss the main empirical findings of the study with respect to the research questions. Secondly, I discuss the implications of the findings with respect to theory, management and policy. Thirdly, I give a brief outline of recommendations for future research including a discussion of limitations encountered during various phases of the studies. Lastly, I end the synthesis with a conclusion section that highlights the current study findings and how they compare with current practice.

6.2 Empirical findings

The empirical findings of the study are chapter specific and are discussed in the respective chapters: 1) *Evaluating relevance of conventional grazing research under global change – A review of drought and grazing studies in semi-arid rangelands* (Chapter 2), 2) *Adding realism and management options to global change experiments: the DroughtAct approach* (Chapter 3), 3) *The Role of Cattle Grazing Management on Perennial Grass and Woody Vegetation cover in Semiarid Rangelands: Insights from Two Case Studies in the Botswana Kalahari* (Chapter 4) and 4) *The Role of Herbivore Impact and Subsequent Timing and Extent of Recovery Periods in Rangelands* (Chapter 5). The findings will be synthesized to answer the research questions asked.

6.2.1 Do existing drought and grazing literature adequately address predicted future climate change scenarios particularly in the context of southern African rangelands?

To answer the above question, I carried out a critical review of drought and grazing literature (Chapter 2) to evaluate the relevance of conventional grazing research in the wake of global environmental change. Whereas grazing and drought research have become global research foci, it became apparent from the review, that the African continent is understudied particularly with respect to drought studies (*cf*. Fig. 2.1). Drought research is not only limited in terms of the number of studies, but also with respect to realistic site-specific drought intensities and extent of the drought treatments (i.e. the duration of drought). On one hand, grazing research is well established and documented in African rangelands, but it also came out clearly, that grazing studies often lack realism with respect to temporal and spatial scale, nature of treatments (e.g. clipping *vs.* grazing), experimental designs (common garden *vs.* in-situ manipulations) and multifactorial approaches that include other elements of ecosystem function such as soil properties. This lack of realism was identified as one of the causes of inconsistencies in grazing research, what may partially explain the continuous debate on superiority of grazing management.

Another key finding of the review was the lack of multifactorial studies that simultaneously manipulate several ecosystem drivers – a recommended approach to better understand the complex nature of dry rangelands (Alba et al., 2017, Flombaum et al., 2017). Here, we found only few studies that implemented this approach; either through theoretical analysis, meta-analysis, modelling and remote sensing, artificial grazing (clipping) or common garden experiments. As already mentioned above, most of these studies lack realism and may need to be repeated or validated under more natural field conditions. However, on one occasion we found a study that evaluated interactive effects of drought and real grazing (by sheep) in the Great Plains of Montana (Heitschmidt et al., 2005), but again this study may not represent African rangelands due to different climate and evolutionary history of grazing.

Through the review, I could further identify approaches that may be implemented in contemporary rangeland research to measure individual and interactive effects of several global change drivers, based on the state of existing knowledge and future projections. In this regard we demonstrated that rigorous and realistic multifactorial experimental designs, that involve standardized and controlled protocols as well as site specific drought treatments, are needed to bridge the knowledge gaps for African rangelands and overcome methodological problems associated with data integration and comparisons (Chapter 2). Thus, present drought and grazing research and the state of knowledge does not adequately address future climate change scenarios predicted for southern Africa due to the limitations outlined above.

6.2.2 How can the knowledge gaps in drought and grazing studies be potentially overcome?

In Chapter 3, we introduced DroughtAct, a large-scale drought and grazing experiment in the rangelands of South Africa’s Limpopo Province (Chapter 3) to address the problems of drought and grazing identified in literature in Chapter 2. The Limpopo area was chosen given its current degradation state as well as predicted future changes likely to aggravate the situation (*cf.* Chapter 1.4), and also to ameliorate the lack of such experiments in savanna rangelands of southern Africa where global environmental changes are expected to have devastating effects (Chapter 1 & 2).

In this chapter I have demonstrated in detail how to implement such an experiment to allow easy replication elsewhere. Using standardized international protocols we implemented a drought treatment informed by the area's precipitation history and went a step further to add a real grazing (by cattle) treatment and options for treatment changes that mimic possible management interventions in the face of droughts (*cf.* Chapter 2.5). With this approach, several biotic and abiotic factors of ecosystem function (e.g. precipitation, grazing and edaphic properties) could be manipulated and evaluated simultaneously. This approach is currently accepted as the gold standard in assessment of complex ecosystems such as dry rangelands (Alba et al., 2017, Flombaum et al., 2017).

Furthermore, we presented bias and artefact check in addition to treatment effects to show that the design and approach has little or no influence from selection bias and equipment artefact but only treatment effect as observed on soil moisture (see Table 3.1 & 3.2) and vegetation dynamics (*cf*. Figure 3.8). Chapter 3 also shows that management interventions such as resting during drought could also be assessed with this experimental approach. In this regard, we demonstrated that, resting periods longer than one season may have damaging effects on the veld even under drought conditions, as a result of an accumulation of standing dead material that inhibits new growth (*cf.* 3.4.4). However, the above is true for veld that is not degraded (i.e. with good cover of perennial grasses) such as the DroughtAct site (*cf.* Chapter 2.1). This response is also consistent with the findings in Chapter 5, drawn from a clipping experiment in semi-arid rangelands of Botswana. Nevertheless, longer recovery periods may be necessary in heavily degraded areas (i.e. areas characterized by bare ground and absence of perennial grasses) (Linstädter, 2009). Thus the DroughtAct approach may be used to overcome missing information in conventional drought and grazing literature and help to develop and test adaptation and mitigation strategies in the face of global environmental change.

6.2.3 How does grazing management influence herbaceous and woody vegetation dynamics?

In this publication (see Chapter 4), we revisited the debate on grazing management (rotational *vs.* continuous grazing; RG, CG) by assessing the role of cattle grazing management on vegetation dynamics of four ranches under different grazing schemes, in semi-arid rangelands of Botswana (Chapter 5). Using this case study approach, I was able to assess long-term effects of CG and RG on tree and herbaceous vegetation on large-scale cattle ranches. This study is one example among many others (*cf.* Chapter 2.2.1) that provide scientific evidence for the superiority of RG over CG with respect to vegetation condition. This study found higher palatable perennial grass cover, lower woody vegetation cover (*cf.* Table 4.1 & 4.2) and higher long-term stocking rates in RG than neighboring CG ranches, suggesting that long-term CG favored woody vegetation establishment over perennial grass cover – a rangeland condition that has been described as degraded (Asner et al., 2004, Reynolds et al., 2007). In addition, the study demonstrated that rangeland health in these regions will not only be achieved by destocking alone, but also demand for uniform grazing and rest periods during the growing season.

Thus, the most important inference drawn from this study comes from the large spatial (large ranches) and temporal (long-term grazing management) scales at which the study was conducted (or which it represents) compared to conventional small scale plot-level grazing studies that have found no differences between RG and CG systems (see Chapter 2.2.1). Also worth noting is the adaptive nature of the management adopted by RG systems surveyed to reduce rigidity in animal movements (Fynn, 2012, Barnes and Hild, 2013). Although this study did not allow evaluation of drought effects, it provides useful insights from realistic grazing scenarios at appropriate scales that allow detection of vegetation changes (Barnes and Hild, 2013). Therefore, this chapter has contributed to the grazing management debate by confirming, that scales and experimental designs are important in influencing the results of grazing studies (Chapter 2). The chapter has particularly provided case study-evidence in support of adaptive RG systems to maintain and/or improve rangeland health.

6.2.4 How does herbivore impact and recovery periods influence rangeland dynamics in semi-arid ecosystems?

In this publication (see Chapter 5), we assessed the role of herbivore impact (i.e. grazing, trampling and defecation) and recovery periods (timing and extent) on herbaceous vegetation at individual tuft and plot-level scales using simulated grazing and hoof trampling in Botswana rangelands (Chapter 4). Using this approach, I was able to evaluate individual and interactive effects of grazing frequency, trampling and dung deposits on herbaceous vegetation thus adding to the mechanistic understanding of grazer effects on vegetation. The first part of the study discovered that perennial grasses require a full growing season's rest to maximize productivity, whereas productivity of palatable species decreases exponentially with previous season clipping frequency suggesting a lagged effect of grazing history. This study also found that less palatable grasses were less resistant to defoliation than the palatable grasses (*cf*. Figure 5.2) underlying the selective forces of grazing.

The second part of the study showed some important interactions of herbivory components where a full season recovery period increased tuft densities while its interaction with dung and trampling increased grass cover (*cf*. Table 5.5 & 5.6). Thus, the results reported in Chapter 5 include a very important aspect of herbivory – the interaction of grazing / resting with hoof trampling and dung deposits – that simulated grazing (i.e. clipping) experiments are lacking. This study attempted to add realism to clipping by simulating hoof trampling using wooden pole and adding dung quantities guided by studies of migratory grazers (*cf*. Chapter 5.2.2.2).

Although the effects of hoof trampling appeared to be less significant on the sandy soils encountered in this study, trampling might have more pronounced effects on harder soils (McNaughton, 1983, Wilson and Tilman, 2002). Whereas the study is quite artificial in that it uses clipping instead of real grazing treatments (Chapter 2), it provided useful information by parting herbivory in its mechanistic components (defoliation, trampling, and nutrient addition) what may not have been feasible with real grazing. Results of this study – particularly those on grazing history, life form and productivity – were consistent with other clipping studies in different continents and regions and also for different species, suggesting the importance of clipping experiments in identifying key factors that need to be evaluated in order to understand grassland responses to grazing (see also Chapter 2.2.2).

6.3 Implications

This PhD study has contributed to existing knowledge and has some theoretical, management and policy implications that may influence further understanding in the subject of rangeland management in the face of global change. These implications are discussed below.

6.3.1 Theoretical

It was demonstrated in Chapter 2 that effects of drought and grazing in dry rangelands are often discussed upon the background of the evolutionary convergence model (Coughenour, 1985, Milchunas et al., 1988). It also came out clear in Chapter 2 that this theory, whereas it provides relevant insights relating to combined effects of drought and grazing (as cited in many drought and grazing studies, *cf*. Chapter 2.3), it has not been sufficiently backed up with empirical data collected on sound scientific grounds. The convergence model states that drought and grazing select for similar (i.e. “convergent”) traits, and hence selective stress of either of these types should increase resistance also to the other.

Although the drought experiment (Chapter 3) was not designed to test the convergence model directly, some of the results of this experiment could be interpreted and discussed along lines of the model. For example the similarity in grazing offtake on drought and non-drought plots as assessed via aboveground biomass (AGB, i.e. ANPP less grazed biomass plus compensatory regrowth), suggests similar tolerance of grazing across these treatments independent of drought, and could be interpreted as consistent with the evolutionary convergence model. However, this needs further investigation. Moreover, grazing offtake may also have been influenced by the farm's grazing management (i.e. grazing duration, intensity and stocking density) (cf. Chapter 3.4.2). Nonetheless, it can be said that, grasses with a long evolutionary history of grazing, such as those in the Limpopo, are expected to show some convergent responses to grazing and extreme drought conditions, the limits of which will be determined by the underlying grazing management.

6.3.2 Management

As already mentioned in the preceding section, the underlying grazing management is very important for any system to function well and it has to be tailored to the observed rangeland condition. For instance, it is evident from experimental data of both clipping and grazing experiments (Chapter 5, Chapter 3) and case studies (Chapter 4) from different sites within the same region, that undegraded rangelands require management that rests grazed veld for a maximum of one season only; even under severe drought conditions. The same studies suggest, particularly that adaptive RG, which promotes uniform grazing and growing season recovery periods, outperforms CG in terms of vegetation performance and hence provision of ecosystem services such as forage provision. Several other studies have provided experimental evidence and rancher-experience, also in support of RG citing circumstances where RG may not outperform

CG with respect to both vegetation and animal performance, as has been argued in rangeland literature (see Chapter 2.2.1).

Another aspect of management, for which this thesis may deliver some implications, is the controversial topic of supplementary feeding. Supplementary feeding is commonly practiced in local rangelands, particularly after years of drought to maintain livestock numbers; a system that has undesired ecological side effects on rangeland condition (Müller et al., 2015). Our finding, that veld needs in-growing season recovery periods, suggest that supplementary feeding should not only be performed after droughts but also during droughts to reduce pressure on the veld, thus allowing parts of the veld to be rested for recovery. In this way, both animal and vegetation may be maintained in a reasonable condition. Thus, where supplementary feeding may not be avoided, it should be included in the grazing management not only to maintain or improve animal condition, but even more so to improve vegetation condition through resting.

6.3.3 Policy

Policies relating to rangelands in general or grazing management in particular often involve short term actions such as reducing stock but evidence from other studies and this thesis (Chapter 4) suggest otherwise. Destocking alone without adaptive grazing management that is informed by sound scientific knowledge of the ecosystem function, may not improve rangeland health. In South Africa for instance, the Department of Agriculture's draft policy on sustainable management of range and forage resources (DoA, 2007) mainly focus on improving productivity through reduced stocking rates, selling more animals, improving breeds and promoting RG (without detailing how to implement it), but does not adequately address issues associated with drought among other livestock sector challenges (Vetter, 2013).

The empirical findings of this thesis suggest that the policy document may be refined in order to emphasize the importance of adaptive grazing management (recovery periods), and should add potential drought mitigation strategies. One such strategy could be to promote subsidies on supplementary feeds during and after drought years, to allow the veld to recover. Another strategy would be to increase livestock prices as an incentive to encourage farmers to sell during and in the post drought year, thus reducing pressure on the rangeland (see Muller et al., 2015).

6.4 Limitations of the study

Whereas the study provided important insights on a subject of global concern, some limitations related to the methodological approaches used and the duration of this PhD study were encountered. For instance, the formal duration of the PhD study is three full-time years, but vegetation responses to both drought and grazing may take longer periods to manifest in the most meaningful ways. According to the requirements of the IDE (DroughtNet, 2015), imposed droughts should last at least four years (mimicking multi-year droughts typical for drylands) after which post drought responses could be assessed. Thus the fourth year of the DroughtAct experiment already falls outside the duration of a typical PhD study. Also, due to logistical constraints, the study did not include assessments of animal condition (e.g. body weight) which is an equally important measurement of rangeland health and productivity.

From a technical point of view, with respect to the DroughtAct experiment (Chapter 3), we did not have procedural controls to test if experimental treatments influenced the responses. In addition, shelter effects on animal behavior (i.e. if animals were attracted to or avoided rainout shelters) were not assessed directly although measurements of GO provided an indirect indication. Furthermore, due to logistical problems (size of the rainout shelters) our study design did not allow for woody vegetation assessments – an important component of savanna biomes with competitive effects on the grass layer.

6.4.1 Grey areas for future research

This study has identified grey areas for future research to further advance our understanding of grazed ecosystems under global environmental change. Based on the limitations of the current study as well as drought and grazing research in general (*cf.* Chapter 2), the following areas have been identified:

- There is need for replication of drought and grazing experiments in multiple sites in the region to avoid drawing conclusions from single site experiments thus increasing generalizability of our findings. These will also help encourage international collaborations and knowledge sharing, thus advancing understanding of determinants of grazing ecosystems under drought.
- The DroughtAct experiment will be continued to allow for assessment of the long-term effects of drought and grazing. In addition to the data presented in this thesis (Chapter 3), there are several other ecosystem responses that will be measured using this approach including forage quality, plant functional traits, plant phenology, community composition as well as different combinations of management interventions.

- A woody vegetation assessment component and procedural controls should be added to drought and grazing experiments to understand interactions of woody plants and herbaceous plants (competitive effects) with drought and grazing.
- More collaborations with cattle ranch owners and conducting ranch-scale grazing studies that include both animal and vegetation assessments are also recommended in future.
- Studies that assess the combined effects of supplementary feeding, grazing and drought are also recommended.

6.5 Conclusions

Generally, this study has advanced the scientific knowledge on grazed ecosystems and how these may be impacted by predicted global environmental changes. First, the study revealed that grazing-related research is well documented in Africa, although it lacks certain levels of realism in terms of study designs and the nature of treatments, whereas relevant drought (and / or grazing) research is lacking. Through a novel experimental approach the study managed to evaluate effects of extreme drought and real grazing simultaneously, contributing to the limited knowledge on combined effects of drought and grazing in African dry rangelands. Key results of this experiment and from a case study of grazing assessment to clipping studies, suggest that optimal vegetation performance in previously undegraded veld, should be obtained by in-growing season resting for durations not exceeding one season, even under extreme drought conditions. The study also demonstrated that rangeland health in degraded areas may not be achieved by destocking alone, but through adaptive management at appropriate scales – an approach that may be achieved on RG rather than CG systems. The clipping experiment further demonstrated lagged effects of grazing history on palatable grass species (i.e. decreases in productivity with increasing clipping frequency) and the significance of other herbivory characteristics (trampling and defecation) in interpretation of clipping results. Thus, the findings of this thesis may be applied to alleviate problems of grazing-related degradation in semi-arid rangelands of Limpopo and elsewhere, and also to develop adaptation strategies for predicted future global change challenges.

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Role of Herbivore Impact and Subsequent Timing and Extent of Recovery Periods in Rangelands☆,☆☆

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trampling

ABSTRACT

The productivity and stability of cattle production on rangelands depends on the maintenance of a dense and productive perennial grass—dominated resource base, which is contingent on appropriate grazing and recovery periods. We investigated the effect of simulated trampling, dung inputs, frequency of defoliation in the previous growing season (grazing history), and timing of recovery periods on various grassland functional responses in two experiments in western and northwestern Botswana. A field-based clipping experiment at the individual tuft scale demonstrated that perennial grasses are most productive when rested for a full growing season, but that productivity of the highly palatable soft leaved *Brachiaria nigropedata* Ficalho & Hiern. decreases exponentially with increasing clipping frequency in the previous season (a lagged effect of grazing history). This species was also more productive in the next season when rested during the early than late growing season. The less palatable needle-leaved *Stipagrostis uniplumis* Licht. ex Roem. & Schult. was less resistant to defoliation than *B. nigropedata* and decreased equally at each clipping frequency regardless of season. A second field-based experiment at the plot scale demonstrated that a full-season recovery period increased tuft densities while its combination with dung increased cover. The effects of hoof trampling on sandy nutrient-poor grasslands appear to be less significant compared with grasslands on fertile soils. Thus, optimal livestock management strategies should aim to promote season-long grazing of both palatable and unpalatable species to disadvantage the less grazing-tolerant unpalatable species and full growing season recovery periods to ensure optimal recovery and future productivity.

Introduction

The effect of grazing on aboveground net primary productivity (ANPP) has been the subject of much debate for a long time (Westoby 1985; McNaughton 1985, 1993; Belsky et al. 1993; Dyer et al. 1993; Painter and Belsky 1993; Hiernaux and Turner 1996; Knapp et al. 2012). While several studies worldwide demonstrated that large herbivore grazing stimulates grassland productivity, otherwise referred to as *overcompensation* (McNaughton 1979, 1984; Noy-Meiyer et al. 1989; Turner et al. 1993; Frank et al. 1998), others argued that evidence supporting the concept of overcompensation in grazed swards is inadequate (Westoby 1985; Painter and Belsky 1993; Hiernaux and Turner 1996; Knapp et al. 2012).

However, the nature and effect of grazing are not monodimensional or linear but vary according to the degree of selectivity by grazers (Morris et al. 1992; Fynn 2012), the intensity of grazing (Briske et al. 2008), the nature and evolutionary history of the grasses (tufted versus creeping; long-term history of herbivory) (Milchunas and Lauenroth 1993; Fynn 2012), and the spatial and temporal scales at which grazing occurs (Frank et al. 1998; Fynn 2012). Thus the effects of grazing on grassland productivity cannot be reliably predicted without knowing specific details of the spatial and temporal scale at which grazing occurs and the types of grasses being grazed. For example, moderate levels of grazing generally stimulate grassland productivity in large-scale migratory ecosystems where the effects of grazing are concentrated and transient (McNaughton 1985; Frank et al. 1998) but reduce productivity (undercompensation) in nonmigratory ecosystems where grazing is often nonseasonal and continuous (Milchunas and Lauenroth 1993; Knapp et al. 2012). Nevertheless, at very high levels, grazing generally reduces productivity irrespective of its spatial and temporal scale across

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landscapes (McNaughton 1979, 1985; Turner et al. 1993; Heirnaux and Turner 1996; Owen-Smith 2002).

A strong theoretical and empirical foundation that underlies current scientific understanding of competitive outcomes among plants under differential nutrient loss rates has been established (e.g., Tilman 1988; Berendse et al. 1992; Tomlinson and O'Connor 2004). Heavy continuous grazing runs down nutrient stores in the plant through removal of nutrients and carbohydrates in grazed tissue (Berendse et al. 1992) but, to a lesser degree, carbohydrate stores because grasses are unable to store much carbohydrate (Danckwerts 1993). This compromises the plant's nutrient economy, resulting in reduced tillering and productivity (Berendse et al. 1992; Tomlinson and O'Connor 2004), which is exacerbated by poor root development and inability of plants to access deep-layer soil moisture and growth-limiting nutrients (Hodgkinson and Bass-Becking 1977). Thus, several studies across three continents have demonstrated that grazing in the previous growing season strongly reduced productivity of grasses in the next growing season (Turner et al. 1993; Ash and McIvor 1998; Knapp et al. 1999; Kirkman 2002). Consequently, long-term selective grazing of palatable perennial grasses results in their ultimate death or competitive exclusion by unpalatable species that do not get grazed much (Morris et al. 1992; Anderson and Briske 1995; Dube and Gwarazimba 2000; Fynn 2012).

Most rotational grazing strategies involve a period of grazing of paddocks followed by a period of recovery, with one to several iterations over the growing season. However, the effectiveness of these within-season recovery periods for restoring effective root systems, nutrient stores, and vigor will likely depend on the availability of soil moisture and nutrients for growth and storage in crowns and roots, which can be recycled to aerial growth in the next season. The fact that nutrients are not mineralized evenly over the growing season but rather in pulsed events (Fierer and Schimel 2002), the bulk of which occurs during spring (Scholes and Sanchez 1990; Higgins et al. 2015), suggests that recovery periods during times of good rainfall, especially during the early growing season, will be more effective for grasses than during drier periods or during the late growing season. Much attention has been given to the effect of defoliation frequency and intensity on grass productivity and community composition (e.g., Danckwerts and Nel 1989; Turner et al. 1993; Anderson and Briske 1995; Hiernaux and Turner 1996; Kirkman 2002), but very little attention has been given to the timing of recovery periods in relation to rainfall and nutrient mineralization and this important aspect needs attention.

Apart from the direct effects of grazing, grazing may also have indirect effects on grasslands, such as through its associated trampling effects and dung and urine inputs, which improve forage quality and grassland productivity by increasing rates of nutrient cycling and removing light inhibiting litter (Knapp and Seastedt 1986), as well as promoting seed burial and establishment (McNaughton 1983, 1985; Georgiadis and McNaughton 1990; Frank et al. 1998). Apart from anecdotal evidence (McNaughton 1983) and some experimental studies (e.g., Wilson and Tilman 2002), little attention has been given to the importance of the effects of physical disturbances of the soil surface by trampling in determining community composition through effects on grass seedling recruitment and aerial litter removal. Thus grazing at the right spatial and temporal scale may provide beneficial ecosystem engineering effects that positively influence ecosystem processes and functioning (Jones et al. 1994), which may then lead to feedback effects on plant composition and productivity (McNaughton et al. 1988).

Our study aimed to determine how the frequency of defoliation (simulated grazing by clipping) and timing of recovery periods affect perennial grass productivity and survival, as well as how the indirect effects of grazing via trampling and dung affect grass biomass and cover. Four hypotheses were postulated: 1) Increasing grazing intensity will reduce grass productivity in subsequent seasons, 2) Timing of recovery periods will influence productivity in subsequent seasons, 3) Dung inputs will increase grass and forb biomass and cover, and 4) Clipping, trampling, and dung will have an interactive influence on cover and biomass in grassland communities.

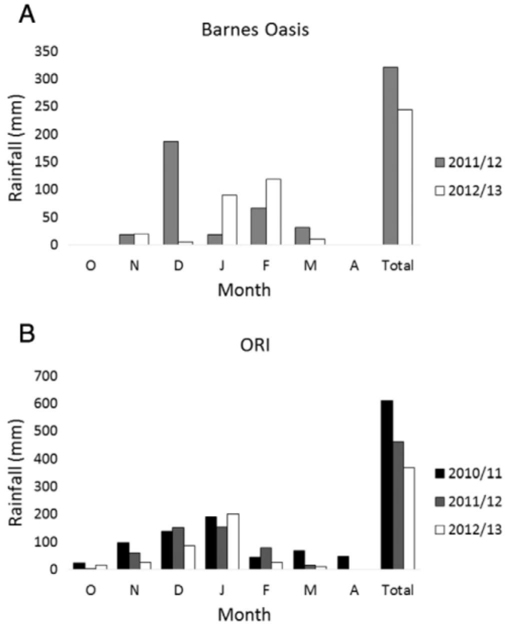

Figure 1. Monthly and annual precipitation data for the 2011/2012 and 2012/2013 growing seasons at the Barnes Oasis ranch in western Botswana (A) and for the 2010/2011–2012/2013 seasons at the Okavango Research Institute (ORI) experiment in northwestern Botswana (B).
Source: Barnes Oasis and ORI records.

Materials and Methods

Study Area

The study was conducted in two separate but complementary experiments in Botswana, examining how clipping frequency affects grass productivity and survival. One experiment was conducted at Barnes Oasis ranch located approximately 24 km southeast of Gantsi Township at 21°53′42.17″S and 21°49′53.58″E. The other study site complementing the Gantsi sites was located on the Okavango Research Institute (ORI) campus situated 15 km northwest of Maun at 19°54′19.29″S and 23°31′51.6″E. Maun and Gantsi fall within the Kalahari ecosystem characterized by deep Kalahari sands and hence have slightly variable but comparable conditions.

The climate in the Gantsi area is arid to semiarid with mean monthly winter minimum temperatures of 5°C and summer highs of 33°C (Bhalotra 1987). Mean annual precipitation (MAP) is 430 mm (Botswana Meteorological Services) with the greater proportion

Table 1
Design for clipping treatments for *Brachiaria nigropedata* and *Stipagrostis uniplumis* tufts during the 2011/2012 and 2012/2013 growing season at Barnes Oasis Ranch in western Botswana. X's indicate months when tufts were clipped. Clipping was done once at the end of the month

Treatment	No. clips	Code	2011/2012				2012/2013			
			Dec	Jan	Feb	Mar	Dec	Jan	Feb	Mar
No rest	4	NR	X	X	X	X	X	X	X	X
Early-season rest	2	ESR			X	X			X	X
Late-season rest	2	LSR	X	X			X	X		
Cut once only	1	COF			X				X	
Full-season rest	0	FSR					X	X	X	X

Table 2
Design for clipping, trampling, and dung treatments during the 2010, 2011, and 2012 seasons at the Okavango Research Institute experiment in northwestern Botswana. The crosses indicate the months when treatments were applied

Treatment	Code	2010						2011						2012					
		J	F	M	O	N	D	J	F	M	O	N	D	J	F	M	O	N	D
Clipped twice every year	C1			X			X			X			X			X			X
Clipped twice every alternate year	C2			X			X									X			X
Clipped five times every year	CF	X	X	X		X	X	X	X	X		X	X	X	X	X		X	X
Control (unclipped)	Cont																		X
Dung addition	D				X						X						X		
Trampling	T			X	X						X						X		

occurring between October and April (Thomas 2002). About 60% of the rainfall occurs between January and March. Rainfall amount and distribution are variable, resulting in recurring droughts (Cole and Brown 1976; Bhalotra 1987). Although total annual rainfall at Barnes Oasis ranch decreased during the study period (from 2011/2012 to 2012/2013), the area received more rain during the early season (December) in 2011 and during the late season (January and February) in 2013 (Fig. 1A). Maun has a relatively similar climate to Gantsi with a slightly higher MAP of 460 mm (Botswana Meteorological Services). The majority of the rainfall occurs between November and March (Ellery et al. 1990; Ellery et al. 1991). However, there was a decrease in annual rainfall during the study period from 2010 to 2013 (Fig. 1B). Temperatures in Maun are relatively high throughout the year with a mean monthly low of 7°C in winter and a high of 34°C in summer (Botswana Meteorological Services).

The soils in Gantsi and Maun are predominantly Kalahari sands, which typically consist of over 95% sand (Thomas and Shaw 1991) with rare bedrock exposures (Cole and Brown 1976). The sands are mostly deep, structureless, and very low in N, P, and organic matter (Skarpe and Bergstrom 1986; Dougill et al. 1998). Vegetation of the Gantsi area is characterized by open shrub savanna with scattered trees and perennial tufted grasses (Skarpe 1986), where *Terminalia sericea* Burch. ex DC. is a common woody species. The grass layer is dominated by *Stipagrostis uniplumis* and *Digitaria eriantha* Steud. (Cole and Brown 1976; van Oudtshoorn 1999). Vegetation around Maun is characterized by *Colophospermum mopane* Kirk ex Benth. woodland on alluvial soils and with patches of *Terminalia sericea* woodland on deep Kalahari sands (Privette et al. 2004), as in the Gantsi region. Nomenclature for all plant names is according to Germishuizen et al. (2006).

Data Collection

Barnes Oasis Ranch Experiment

Two experimental sites within 2 km of each other (and hence with similar growing conditions), one dominated by *S. uniplumis* and the other by *B. nigropedata*, were identified on Barnes Oasis ranch. These C4 grass species were selected because they are the most dominant species on the ranch (Mudongo 2014) and are good examples of a hard needle-leaved, less palatable species and a soft-leaved, highly palatable species, respectively (van Oudtshoorn 1999). Each experimental site was fenced off with a wire-strand fence with additional fine-mesh chicken wire to protect grasses within the experiment from grazing. The chicken mesh wire was also buried about 20 cm below ground level to keep hares out. The experiment was set up as a random complete block design with 10 blocked replicate tufts of the dominant species at that site. Five clipping treatments (Table 1) were randomly allocated to five tufts of each grass species per block. We selected tufts that were not < 5 cm in basal diameter. Neighboring plants were never close enough to cause shading of experimental tufts and hence were not clipped. Each clipping treatment was denoted by color-coded steel rods, which were used to mark the selected tufts. While clipping was used to simulate grazing by cattle, we realize that cattle rarely graze tufts to low levels, so the clipping represented very intense grazing. All marked tufts were first clipped down (about 5 cm above the ground) in the dry season (September 2011) to remove senescent material before the growing season for accurate measure of aboveground productivity.

Clipping treatments were done in two growing seasons commencing from December 2011 to March 2012 for the first season and December 2012 to March 2013 for the second season (see Table 1). Tufts were clipped at 5 cm above the ground with the use of clippers. Before the first clipping event, the circumference of each tuft was measured with a flexible measuring tape. This would then be used to calculate the initial tuft area, with productivity being expressed per unit tuft area to standardize comparisons. After each clip, all material was collected in brown paper bags, oven-dried at 60°C for 48 hours, and weighed for biomass. From the treatments that were clipped, productivity was taken as a means of the summed monthly clips in the season.

Productivity in the full season rest (FSR) treatments was measured in the second year by sorting plant material into previous season's dead (oxidized) and current season (green and brown) (e.g., Knapp et al. 2002). Productivity of each surviving tuft was calculated as biomass per initial tuft area to standardize for different tuft sizes. In the first season of the Barnes Oasis ranch experiment, cattle twice managed to break through the fence of the *B. nigropedata* experiment and some experimental tufts were moderately grazed. Owing to the high replication of treatments (10 blocks), however, potential confounding effects of these two grazing events do not seem to have overridden clipping treatment effects, which constituted a far more severe defoliation.

ORI Clipping/Dung/Trample Experiment

Another clipping experiment that had been running in a homogeneous area of grassland at the ORI from November 2009 to February 2013 was used to complement the experiment at Barnes Oasis Ranch. Experimental treatments were applied in the wet seasons of 2009–2010, 2010–2011, and 2011–2012 with assessments of treatment effects being done in 2013. Grazing was simulated by clipping. A three-factor, random, complete block design of 16 treatments replicated seven times to make 112 plots was used in the experiment (four clipping × two soil trampling × two dung addition, Table 2). Plots measured 1.5 × 1.5 m, with 1 m—wide walkways between rows of plots and 0.75-m spacing between plots in a row. The clipping treatments were 1) clipped at the end of December and March every year (C1); 2) clipped at the end of December and March every alternate year (C2); 3) continuously clipped at the end of November, December, January, February, and March every year (CF) (November not clipped if rains came late); and 4) unclipped control (Cont). Soil trampling (T) and dung addition (D) treatments were applied (see Table 2).

In 2010, soil trampling was simulated by chipping the soil surface with an axe but was changed to stamping and breaking the soil with a 6-cm diameter wooden pole (considered similar to the impact of cattle hooves) at the end of March and October in 2010. In 2011 and 2012 it was only carried out in October (see Table 2). Dung inputs involved addition of 200 g of crushed cattle dung per plot, where the amount was calculated from studies of dung deposition in East Africa (David Augustine, unpublished data). An amount equivalent to 6 months of deposition was chosen to represent the time migratory grazers would spend in a seasonal range. Dung inputs were applied just before the

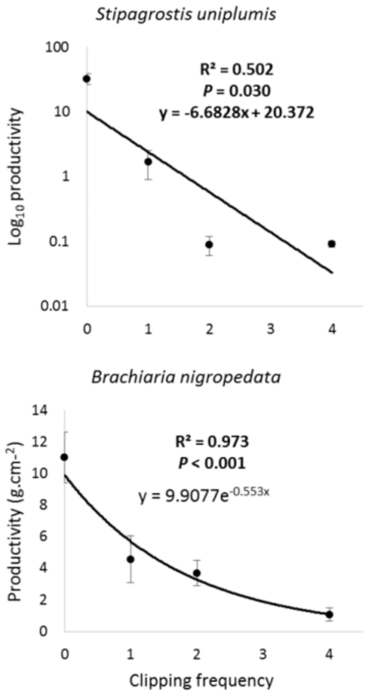

Figure 2. Response of *Brachiaria nigropedata* and *Stipagrostis uniplumis* second-season productivity to first-season clipping frequency during 2011/2012 and 2012/2013 growing seasons at Barnes Oasis ranch in western Botswana. The *P* values (significant values with $P < 0.05$) and R^2 are from nonlinear and linear (*B. nigropedata* and *S. uniplumis*, respectively) regressions of 50 individuals ($n = 50$) of each species.

soil trampling treatment in October to allow for the effect of trampling on dung incorporation in the soil.

In February 2013 the aerial cover of each grass species and forbs, bare ground, and litter cover, as well as aboveground biomass, were measured in each plot. Tuft density was recorded in each plot by counting the number of grass tufts in a 0.5 × 0.5 m quadrat placed in the center of each plot (to avoid edge effects). Aboveground biomass was determined by harvesting all plants in the 1-m^2 quadrat and separating into forbs and grass. The aerial cover of each grass species in a plot was determined by giving a visual percentage estimate of its cover within the plot. All harvested plant components (forbs, current-year's grass, and previous-year's dead material were oven-dried at 60°C for 48 hours and weighed. Rainfall data for the period of the study were obtained from the Barnes oasis and ORI onsite weather stations.

Table 3
Mean (± SE) second-year productivity of *Brachiaria nigropedata* and *Stipagrostis uniplumis* under different first-season clipping treatments during the 2011/2012 and 2012/2013 growing season at the Barnes Oasis ranch in western Botswana. Means with a different letter in a column indicate significant differences based on multiple comparisons of Tukey's post hoc test

		Brachiaria nigropedata	*Stipagrostis uniplumis*
Treatment	No. Clips	Productivity ($g \cdot cm^{-2}$)	Productivity ($g \cdot cm^{-2}$)
No rest	4	1.08a ± 0.41	1.98a ± 0.39
Early-season rest	2	5.29b ± 1.29	0
Late-season rest	2	2.15a ± 0.69	0
Cut once only	1	4.57b ± 1.46	1.72a ± 0.81
Full-season rest	0	11.0c ± 1.61	32.8b ± 6.42

Data Analysis

For both experiments, significance of difference between treatments was obtained by carrying out a linear mixed-effects model (using treatments as fixed effects and block as a random effect) with analysis of variance (ANOVA) and Tukey HSD multiple comparisons in R. At the Barnes Oasis experiment, initial tuft size was used as a covariate in the ANOVA. We tested the effect of clipping frequency in the first season (zero, one, two, or four clips) on second-season productivity of *B. nigropedata* and *S. uniplumis* by performing a nonlinear and linear regression, respectively, on a sample size of 50 individuals of each species ($n = 50$). The control in this analysis (zero clips in first season) was the full-season rest treatment (see Table 1) where previous-year's dead material that had accumulated in the full rest of the first season and was clipped in the December clip of the second season was discarded, as we were only interested in second-season growth. The previous year's dead material (gray in color) could easily be distinguished from second-season growth, which was either live (green) or senesced (brown). After the first clip (December), only second season's growth remained for the January, February, and March clips. Thus, none of our productivity assessments were based on using previous-year's dead material, where some material may be lost through decomposition, which ensured all treatments in the analysis were comparable (second seasons growth only). Normality of the data was tested by Shapiro-Wilk test, whereas homogeneity of variance was checked by examining residuals plots. A binary logistic regression analysis was conducted to predict the odds of survival of tufts using treatment and tuft area as predictors. The test predicts the probability that the dependent variable is either a success or failure using a Wald statistic to assess the significance of coefficients. Data violating assumptions of ANOVA and regression were log transformed.

Results

Barnes Oasis Ranch Experiment

Second-season productivity for both *B. nigropedata* and *S. uniplumis* decreased with increasing first-season clipping frequency, but the decline for *S. uniplumis* was much more abrupt and dramatic at any clipping frequency (see Fig. 2). The full-season rest (FSR) treatment resulted in the highest productivity for both *B. nigropedata* and *S. uniplumis* in the second season (Table 3). A single-cut (COF) treatment reduced productivity of *B. nigropedata* by more than 50% in comparison with the FSR treatment (see Table 3). For *B. nigropedata*, the early-season rest (ESR) treatment resulted in greater productivity than the late-season rest (LSR) treatment despite both treatments having the same clipping frequency (see Table 3).

While clipping treatment did not influence tuft mortality in *B. nigropedata*, the no-rest (NR) and COF treatments made a significant contribution to *S. uniplumis* tuft mortality prediction (Table 4). There were 11% and 44% chances of survival of *S. uniplumis* tufts under the NR and COF treatments, respectively (see Table 4). Tuft area did not influence mortality in either species ($P > 0.05$, see Table 4).

ORI Clipping/Dung/Trample Experiment

Clipping treatment and its interactions with dung and trampling had significant effects on grass cover and tuft density ($P < 0.05$, Table 5). Dung alone did not influence herbaceous vegetation variables ($P > 0.05$, see Table 5) whereas trampling influenced forb cover ($P < 0.05$, see Table 5). Cover of forbs increased from 21.6 ± 3.2 in control treatments to 28.4 ± 2.96% in trampled treatments. Grass cover was highest (> 70%) in plots clipped in alternate years (receiving a year-long recovery period) and receiving dung (C2D) but was comparable with plots clipped every year combined with trampling and dung additions (C1DT) and those plots clipped in alternate years with dung and trampling (C2DT and C2 each at 61.7%, Table 6). Tuft density was highest in

Table 4
Prediction of survival and death of tufts of *Brachiaria nigropedata* and *Stipagrostis uniplumis* using clipping treatment and tuft area as predictors from the Barnes Oasis experiment in western Botswana. The odds ratios and associated *P* values (significant values with $P < 0.05$ in bold font) are from a binary logistics regression

		Brachiaria nigropedata					*Stipagrostis uniplumis*					
Predictor	Died	Survived	Wald	EXP (B)	Odds ratio	*P*	Died	Survived	Wald	EXP (B)	Odds ratio	*P*
No rest	4	6	0.92	0.38	0.68	0.341	9	1	8.7	0.01	0.11	**0.004**
Early-season rest	1	9	0.38	2.25	0.92	0.543	5	5	3.2	0.08	0.49	0.052
Late-season rest	0	10	0	NA[1]	0.99	1.000	0	10	0	NA	0.99	1.000
Cut once only	1	9	0.38	2.25	0.92	0.543	6	4	4.4	0.06	0.44	**0.033**
Full-season rest	0	10	0	NA	0.99	1.000	0	10	0	NA	0.99	1.000
Tuft area	7	53	2.76	1.02	0.80	0.100	21	39	1.88	1.01	0.70	0.172

[1] NA indicates not applicable.

plots clipped in alternate years (C2) and did not differ when dung (C2D) or a combination of dung and trampling (C2DT) was added (see Table 6). Aboveground grass biomass was highest in control plots and lowest in plots clipped and trampled every year (C1T) (Table 7). However, clipping twice every year (C1) and clipping twice every alternate year (C2) yielded comparable grass biomass with the control treatments (see Table 7).

Discussion

Several key results from the tuft clipping experiment on Barnes Oasis Ranch provide important insights and contributions to the debate on grazing effects on compensatory growth in rangelands (e.g., McNaughton 1985; Westoby 1985; Painter and Belsky 1993; Knapp et al. 2012). Our experiment demonstrated that productivity of *B. nigropedata* and *S. uniplumis* decreased exponentially and linearly, respectively, with increasing clipping frequency (see Fig. 2), such that second season productivity was greater for tufts not clipped in the first season (FSR) than tufts clipped in the first season (see Table 3). This is perhaps because by the second growing season the tufts clipped over the first growing season (NR, ESR, LSR, and COF) had incurred reoccurring loss of photosynthetic tissue. Loss of photosynthetic tissue results in losses of photosynthetic-derived carbon and growth-limiting nutrients, which would have been recycled and used for regrowth in the next season (Berendse et al. 1992; Danckwerts 1993; Tomlinson and O'Connor 2004). In addition, frequent and intense grazing may strongly reduce both root biomass and root depth in grasses and sedges (Archer and Tieszen 1983; Danckwerts and Nel 1989; Snyman 2009), which will likely negatively impact nutrient storage and moisture and nutrient uptake for regrowth in the next season. Our clipping height (~5 cm) represented severe defoliation. Thus, our results demonstrate a negative lagged effect of grazing/clipping history on the current season's grassland productivity.

Almost identical results to our experiment were obtained in a clipping experiment in tallgrass prairie, which showed that *Schizachyrium scoparium* Michx. increasingly undercompensated in the second and third growing seasons of clipping (Turner et al. 1993). Relative growth rates of *Andropogon gerardii* Vitman. were much greater for plants rested in the previous year compared with those grazed in the previous year (Knapp et al. 1999). Similarly, sour veldt grasses grazed in the previous growing season were much less productive in the next season than grasses rested during the previous season (Kirkman 2002), as was the case in Australian grasslands (Ash and McIvor 1998). Thus, although our experimental design does not allow us to examine overcompensation directly, our results suggest that overcompensation will likely only be observed in tufted perennial grasses (not lawn grasses, which are more resilient under grazing owing to lower loss rates) that have had sufficiently long recovery periods after grazing in the previous growing season to enable full recovery of nutrients lost to grazing and development of deep and strong root systems, thereby enabling vigorous regrowth after grazing in the next growing season (reducing lagged effects of grazing history). Under compensation as a result of grazing history, induced lagged effects on productivity were clearly demonstrated by Turner et al. (1993).

Another important result was that *B. nigropedata* showed a seasonal effect of clipping frequency such that tufts rested early in the first growing season, such as in the ESR and COF treatments, were more productive in the second season than tufts rested late (LSR) (see Table 3). This is despite the lower rainfall during the early months (December/January) than later months (February/March) of the 2012/2013 growing season (see Fig. 1). A possible reason for this is that the late growing season is not favorable for grasses to recover nutrients lost to grazing, where peak mineralization may occur in the early growing season (Higgins et al. 2015). This is also linked to the observations that mineralization rates are much higher after rewetting of dry soils (Scholes and Sanchez 1990; Fierer and Schimel 2002), where soils are driest at the start of the early growing season after a long dry season in African savannas. By contrast with *B. nigropedata*, *S. uniplumis* was reduced by each clipping frequency to a similar level irrespective of season, suggesting that *S. uniplumis* is intolerant to severe defoliation at any frequency regardless of season.

While soil moisture may also limit growth in semiarid environments, C4 grasses have an increased water use efficiency that allows them to survive under dry conditions (Edwards et al. 2010), suggesting that early-season nutrient fixation and soil moisture conservation are

Table 5
The main effects of clipping treatment, dung addition, trampling, and their interactions on grass cover, standing biomass, tuft density and forb cover measured during February 2013 at the ORI experiment in northwestern Botswana. The F and *P* values (significant values with $P < 0.05$ in bold font) are from an analysis of variance of mixed effects model

Source		Grass cover		Standing grass biomass		Tuft density		Forb cover	
	Df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Clipping treatment	3	1.63	0.211	3.13	**0.045**	13.5	< **0.001**	0.14	0.812
Dung	1	0.58	0.463	0.01	0.943	0.45	0.511	0.01	0.980
Trampling	1	1.87	0.200	0.02	0.888	0.01	0.932	5.44	**0.041**
Clip × Dung	3	3.69	**0.033**	2.44	0.090	8.92	< **0.001**	0.27	0.853
Clip × Trampling	3	5.49	**0.011**	3.40	**0.041**	8.23	< **0.001**	0.81	0.500
Dung × Trampling	1	1.62	0.230	1.57	0.233	0.03	0.864	2.77	0.131
Clip × Dung × Trampling	3	9.65	< **0.001**	0.47	0.700	5.23	**0.010**	0.98	0.420

Table 6

Mean (± SE) grass cover and tuft density in response to clipping and its interactions with dung and trampling measured during February 2013 at the Okavango Research Institute experiment in northwestern Botswana. Means with a different letter in a column indicate significant differences ($P < 0.05$) based on multiple comparisons of Tukey's post hoc test. Only those treatments with significant effects are shown

Treatment	Grass cover (%)	Tuft density[1] (no • m^{-2})
Clipped twice every year (C1)	55.8c ± 1.05	17.0c ± 0.24
Clipped twice every alternate year (C2)	61.7dc ± 1.16	18.9d ± 0.33
Clipped five times every year (CF)	53.1bc ± 1.00	16.3bc ± 0.29
Control (Cont)	39.3a ± 0.74	14.8a ± 0.18
C1 × Dung (D)	55.9c ± 1.05	16.9c ± 0.25
C2 × D	72.7d ± 1.37	18.9d ± 0.35
CF × D	51.9bc ± 0.98	16.1b ± 0.30
Cont × D	47.1ab ± 0.88	14.7a ± 0.22
Cont × Trample (T)	27.6a ± 0.60	15.1a ± 0.25
C1 × D × T	63.0dc ± 1.19	18.0c ± 0.44
C2 × D × T	61.7dc ± 1.16	19.1d ± 0.36
CF × D × T	56.0c ± 1.06	16.3bc ± 0.29
Cont × D × T	26.7a ± 0.64	15.5ab ± 0.30

[1] Values were log transformed for statistical analysis.

critical in dry, nutrient-poor environments. This is a key and novel result that links grass productivity under clipping to the timing of rest during the growing season, which has not been demonstrated in previous studies, particularly in sandy dystrophic soils.

We suggest that N economy in grasses provides a unifying explanation of our observations on grazing history effects and timing of resting/grazing on the next growing season's productivity because both of these factors likely affect N uptake and storage (grazing removes N, while early season resting falls in the period of peak N mineralization), but this will require further investigation. For example, dry season grazing, when grasses are dormant and have translocated N to below ground stores, has much less negative effect on productivity in the next season compared with wet season grazing, where grasses would lose more N to grazing (Ash and McIvor 1998). Similarly, grassland productivity can be linked to as far back as the previous 4 years' rainfall events (Wiegand et al. 2004), which control mineralization pulses in soils (Scholes and Sanchez 1990; Fierer and Schimel 2002; Higgins et al. 2015).

The other key finding of our experiment was that the palatable *B. nigropedata* was much more tolerant of clipping than the less palatable *S. uniplumis* (see Table 4) as observed in clipping experiments comparing palatable and unpalatable species in North America (Anderson and Briske 1995) and South Africa (Morris and Tainton 1993). More preferred palatable grasses such as *B. nigropedata* may be more tolerant of clipping than tough-leaved grasses such as *S. uniplumis*, but they are often replaced by these less preferred grasses under poor grazing management practices (Morris et al. 1992; Anderson and Briske 1995). The palatable grasses are selectively eaten and overgrazed, which, as we demonstrated, leads to declining productivity and ultimately replacement by less preferred species (Morris et al. 1992; Anderson and Briske 1995). However, grasses that are adapted to a lack of disturbance in the form of grazing or fire have developed tolerance traits such as slow growth rates and shade tolerance to enable them to withstand reduced light levels and increased litter (MacDougall and Turkington 2004; Fynn et al. 2011) but are less tolerant of clipping/grazing (Morris and Tainton 1993).

Table 7

Mean (± SE) standing grass biomass in response to clipping and its interactions with trampling measured during February 2013 at the Okavango Research Institute experiment in northwestern Botswana. Means with a different letter in a column indicate significant differences ($P < 0.05$) based on multiple comparisons of Tukey's post hoc test. Only those treatments with significant effects are shown

Treatment	Standing biomass[1] (g • m^{-2})
Clipped twice every year (C1)	71.7abc ± 1.66
Clipped twice every alternate year (C2)	72.5bc ± 1.78
Clipped five times every year (CF)	71.0ab ± 1.82
Control	76.5c ± 1.33
C1 × Trample (T)	67.4a ± 1.48
C2 × T	69.7ab ± 1.52
CF × T	70.6ab ± 1.92
Control × T	77.4c ± 1.42

[1] Values were log transformed for statistical analysis.

The similarity of the results of our study with several others on grazing history (Turner et al. 1993; Ash and McIvor 1998; Knapp et al. 1999) and life history (Morris and Tainton 1993; Anderson and Briske 1995) effects on grassland productivity, despite regional and intercontinental separation and different grass species dominants, demonstrates that grazing history and life history effects are key general factors that need to be accounted for in understanding grassland productivity responses to grazing. Thus, we suggest that when taking into account 1) the length of recovery after clipping/grazing (short-term grazing history), 2) the evolutionary history (grazing tolerance), and 3) the life history (palatable, soft leaved vs. unpalatable, needle leaved) of the dominant grass, the compensatory response of grasslands (overcompensation vs. undercompensation) under grazing becomes a robust and predictable concept. These results support hypotheses 1 and 2.

In accordance with our findings that season-long resting (alternate year clipping) increased grass productivity, at the ORI experiment we demonstrated that alternate-year clipping (C2) increased tuft densities irrespective of dung addition and trampling, whereas grass cover increased when dung was added (see Tables 5 and 6). While soil trampling has been found to increase seedling establishment (Wilson and Tilman 2002) and hence high seedling densities (McNaughton 1983), this was not the case in our study. A possible explanation of this difference is that our study was conducted in sand veld environments, where the effects of hoof trampling may be less pronounced than on hard veld environments.

Although no attention was paid to the soil type in terms of its inherent pattern of nutrient availability, the response is interpreted to have taken place in poor sands on which the rates of regrowth are accordingly expected to be slow—grasses on more fertile soils may have been less susceptible to mortality under clipping than on these sandy soils, but it is expected that productivity responses to clipping history would have been the same (e.g., Turner et al. 1993; Kirkman 2002).

Implications

Our results confirmed that a full growing season recovery period is far superior to partial resting within the growing season, as noted elsewhere by Kirkman and Moore (1995), Zacharias (1995), and Briske et al. (2011). The observation that even one cut during the growing season reduced productivity in the next growing season by half relative to a full growing season recovery suggests that partial recovery periods (early or late growing season recovery periods) are not optimal in semi-arid, nutrient-poor rangelands but rather that a full growing season recovery period is the best management strategy in these rangelands.

Most rotational grazing systems worldwide include several grazing and recovery periods within each paddock over the growing season. Our data suggest that rotational resting (deferred resting) in which some paddocks are grazed and others rested over the entire growing season (e.g., Kirkman and Moore 1995) is a superior approach to grazing management. However, this may be relative to plant productivity of C4 bunch grasses and limited to the environmental conditions characterizing sandy nutrient-poor rangelands, although other studies on fertile soils and under high rainfall have drawn the same conclusions (Zacharias 1995). Our observations that less palatable, needle-leaved grasses were less tolerant of clipping than palatable soft-leaved grasses suggests that managers can aim to reduce the abundance of less palatable grasses by use of nonselective grazing techniques, which encourage grazing of both palatable and unpalatable species (e.g., season-long grazing after fire to maintain unpalatable grasses in a short, higher-quality state).

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The Role of Cattle Grazing Management on Perennial Grass and Woody Vegetation Cover in Semiarid Rangelands: Insights From Two Case Studies in the Botswana Kalahari

By Edwin I. Mudongo, Tsholofelo Fusi, Richard W.S. Fynn, and Mpaphi C. Bonyongo

On the Ground

- We assessed the long-term effects of continuous and rotational grazing on grass and tree dynamics on adjacent ranches in the semiarid Kalahari of western Botswana.
- Rotationally grazed ranches had higher grass cover with more perennial grass species, higher grazing value (and capacity), and higher long-term stocking rates than their continuously grazed neighbors. Tree cover tended to be higher on continuously grazed ranches, suggesting that long-term continuous grazing reduced grass production and favored establishment of woody vegetation.
- Improvement in semiarid rangeland health and production is unlikely to be achieved simply by reducing stocking rates; uniform grazing and growing season recovery periods are essential.
- These and other case studies suggest that benefits of grazing strategies likely depend on scale and adaptive management. Future research should be at larger spatial and temporal scales.

Keywords: continuous grazing, grazing capacity, grazing value, rotational grazing, stocking rate.

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Grazing management practices are broadly defined as reoccurring periods of grazing, resting, and deferment of pastures.[1] For simplicity grazing systems are categorized into two broad types: continuous grazing (CG), which involves season-long grazing of the entire management unit, and rotational grazing (RG), which involves moving a herd through multiple pastures within a matrix of paddocks in varying phases of recovery from grazing.[2] Rotational grazing practices are meant to increase grass and animal production, promote more uniform grazing, and maintain favorable grass species composition.[1,3]

Inappropriate grazing practices may result in undesirable vegetation change in rangelands including an increase in woody vegetation and a decrease in perennial grass species leading to reduced carrying capacity.[4] Productive perennial grasses exert strong competitive effects on woody species, thereby greatly retarding their growth.[5] The effects of reduced competition by the grass layer may be exacerbated by reduced fire intensity and frequency, leading to unimpeded woody plant establishment and growth.

Rangeland researchers and managers worldwide continue to debate the efficiency of continuous and rotational grazing practices in maintaining rangeland vegetation and livestock production.[3] Meta-analyses of grazing experimental data have found little or no advantages of RG over CG, with stocking rate rather than grazing system consistently emerging as the most important management factor determining range condition and animal performance.[6] However, Teague and colleagues identified problems associated with small-scale grazing experiments and provided ranch-scale evidence for the benefits of adaptive RG over CG.[3] These authors argued that results from grazing experiments that have relatively small spatial and temporal scales bear little resemblance to the effect of long-term ranch-scale management.

That notwithstanding, small scale experimental research has demonstrated that defoliation of grasses via clipping or grazing reduces their productivity in subsequent years,[7,8] indicating that grasses need periods of non-grazing during the growing season to allow them to recover nutrients lost to grazing. Without sufficient time for recovery, repeatedly grazed perennial grasses will eventually be replaced by ungrazed (less palatable) neighbors and annual grasses[7–9] especially on infertile sandy soils, where recovery of nutrients lost after grazing is more difficult than on fertile soils. These shifts in species composition to plants of lower grazing value, and in dominant life form from perennial to annual, may result in a decline in carrying capacity.[4]

In western and northwestern Botswana, cattle ranching is the main land use practice and an important economic and livelihood strategy in the rangelands.[10] Grazing practices in this area vary from communal areas without a defined system of grazing to commercial ranching in fenced private farms with distinct grazing practices.[11] While there is uncertainty over the efficacy of RG compared with CG,[2,6] both systems (at different levels of intensity) are widely used by ranchers. However, signs of undesirable rangeland conditions have been reported in both commercial cattle ranches and communal areas in this area.[12] In an attempt to monitor and improve rangeland condition in these areas, local government authorities set stocking rates guided by carrying capacities according to the amended grazing policy on agricultural development of 1991.[13]

To acquire more ecological understanding of the dynamics of grasses and woody vegetation between the grazing practices, we conducted two studies on two pairs of adjacent ranches, where in each pair one practiced RG and the other CG, in all cases for many (12-21) years in western and northwestern Botswana. Our objective was to determine the effect of RG vs. CG on perennial grass cover, composition, biomass, and woody vegetation cover. We hypothesized that persistence of perennial grasses and woody vegetation cover would differ with ranches subjected to RG showing significantly higher persistence of perennial grasses and lower woody vegetation cover. We expected to provide insights that would advise policy and ranchers on grazing management strategies in semiarid rangelands particularly on sandy infertile soils.

Study Area

We selected two pairs of adjacent ranches, where in each pair, one practiced RG and the other CG, at two separate sites in the Kalahari ecosystem of Botswana. Both Gantsi and Ngamiland district have a semi-arid climate with cold dry winters and hot wet summers with a mean annual precipitation of 430 mm and 460 mm, respectively.[14] Soils at both study sites are deep Kalahari sands with low nutrients and organic matter content.[15] One site was at Farm 122 and Farm 120-121 in Gantsi District in western Botswana (21°53'42.17"S and 21°49'53.58"E). The other site was at Farm 12 and Farm 11 of the Hainaveld ranches in Ngamiland District in northwestern Botswana (20°26'30.05"S and 23°25'39.9"E).

Gantsi is characterized by open shrub savanna with scattered trees and perennial tufted grasses, dominated by silky bushman grass (*Stipagrostis uniplumis)* and common finger grass (*Digitaria eriantha)*. Vegetation of the Hainaveld ranches is dominated by raisin bush (*Grewia* spp.) and silver terminalia (*Terminalia sericea*) woodland with grass layer characterized by *Digitaria eriantha* and love grasses (*Eragrostis* spp.).[16] The annual recommended stocking rates for Gantsi and Hainaveld, as determined by the Department of Animal Health, and production during the time of survey were 19 ha per livestock unit (LSU, where a LSU is equivalent to a mature cow) and 17 ha/LSU, respectively. However, the recommended stocking rates vary from year to year depending on rainfall and vegetation conditions.

Management Strategies on the Ranches

While some of the ranches we assessed kept detailed records, we acknowledge that information on past management strategies on some of the ranches beyond 15 years was in most cases not available, and as a result we depended on anecdotal information by the ranch owners.

Gantsi – RG

Farm 120-121 (18,800 ha) is a private commercial cattle ranch with a network of fences dividing it into 64 paddocks with eight water points. The water points are located in the center of a wagon wheel pattern of radiating fences of paddocks. It has an advanced intensive grazing system that involves moving multiple herds of cattle (main herd >2,000) to graze each paddock for a week and then allowing the grazed paddock to recover for at least three months. The system is more than just a simple rotation of cattle between paddocks as it also involves pasture assessments in individual paddocks prior to grazing. There were 3,554 mature cattle on the ranch during the study period and this equated to 5.3 ha/LSU, which was more than three times the recommended stocking rate of the region (19 ha/LSU). The stocking rate and the system of grazing had been maintained for 21 years since 1990 (Dudley Barnes–the ranch owner, pers. comm., October 2011).

Gantsi – CG

Farm 122 (15,000 ha) is also a privately owned commercial cattle ranch in Gantsi adjacent to Farm 120-121. The ranch is not divided into any paddocks and it has only one water point located at the northwestern corner. It has been continuously grazed at low stocking densities for at least 15 years since 1996. Information from the Gantsi veterinary department (although it has gaps on some years) indicates that cattle numbers have fluctuated from 745 (20.1 ha/LSU) in 1996 to 582 (25.8 ha/LSU) in 2004. In 2005 ownership of the ranch changed but grazing management remained unchanged until 2011 (time of this survey). During this time, there were 400 head of cattle in the ranch (37.5 ha/LSU), which is about half the recommended stocking rate (19 ha/LSU).

Hainaveld – RG

Farm 12 (5,000 ha) is a commercial cattle ranch at Hainaveld practicing a less intensive system of RG. The ranch is divided into six paddocks where cattle spend two months in each paddock. Three paddocks (half of the ranch) are always grazed in the wet season, and the other three in the dry season. Paddocks that are grazed in the dry season get a full wet season recovery period. Each of the paddocks grazed in the wet season gets at least three months of recovery time either early or late in the growing season depending on when it was grazed, and remains ungrazed throughout the dry season. During the time of survey, there were 450 head of cattle at ca. 11.1 ha/LSU (Sekeletu pers. comm., June 2015). The average stocking density over a 12-year period since 2002 leading up to the study was 13 ha/LSU.

Hainaveld – CG

Farm 11 ranch (5,000 ha) practices CG at ca. 22 ha/LSU. The ranch does not have a defined grazing practice and one herd of cattle graze the entire ranch without paddocks throughout the season. The grazing practice has been maintained for more than 15 years since 1999. Records from the animal health department indicate that the ranch has been stocked at an average of 20 ha/LSU over a period of 15 years (1999–2014).

Vegetation Assessment Methods

We used a fenceline contrast approach to survey vegetation differences between the ranches at both sites. However, we used different vegetation assessment methods at the two sites. For grazing value (palatability) and life form (perennial or annual) of grasses, we followed the classification of van Oudtshoorn. We considered both research and management levels of confidence associated with statistical significance of differences on vegetation dynamics between grazing management types for decision-making purposes.

We conducted the Gantsi contrast in February 2012 along the 7 km eastern boundary of the RG farm and the adjacent CG farm. We assessed grass cover, composition, and standing biomass (live and dead) using the line intercept and quadrat sampling technique in pairs of adjacent transects such that each pair consisted of one transect on the RG and the other on the CG ranch (Fig. 1). We used remotely sensed images of the ranches to compare woody vegetation cover on the two ranches from tree crown areas calculated on 10 paired plots where in each pair one plot was in the RG and the other in the CG ranch (Fig. 1). A full description of the plots and transects layout and treatments is available in the supplemental material (http://dx.doi.org/10.1016/j.rala.2016.07.001).

We carried out the Hainaveld contrast in June 2015, along a section of the RG ranch where the paddock was grazed during the dry season. We surveyed grass and woody vegetation cover along the shared fenceline of the RG and the CG ranch using the variable quadrat method for woody species and the quadrat method for grass species (see online supplemental material). We laid ten pairs of quadrats perpendicular to and 20 m from the fenceline at 500 m intervals.

Refer to the online supplemental material for a full account of the statistical tests and significance levels of differences between the ranches for both research and management decision-making purposes.

Results of Grazing Management

Refer to Table 1 for the response of woody vegetation cover and grass dynamics to grazing management. Total grass cover and perennial grass cover at Gantsi were higher on the RG while annual grass cover was higher on the CG ranch. Similarly, at Hainaveld, total grass cover and perennial grass cover were higher on RG than CG ranch, while annual grass cover did not differ between the ranches. Aboveground biomass (current year and previous years dead) and species diversity did not differ between the RG and CG but species richness was higher on the CG ranch in Gantsi. However, at Hainaveld, the RG ranch had higher grass species diversity than the CG ranch with the same number of species.

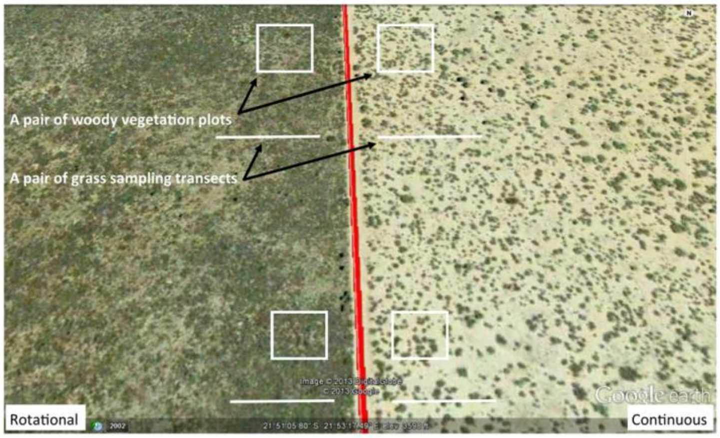

Figure 1. A Google Earth image showing pairs of woody vegetation assessment plots and grass sampling transects drawn along a fenceline (red line) dividing a rotationally grazed and a continuously grazed ranch of Gantsi district in western Botswana. Plots in each pair measure 40 × 40 m, and pairs are 500 m apart.

Table 1. Cover by life form, grass biomass, species richness, and diversity on adjacent ranches practicing continuous or rotational grazing, in two districts of western Botswana

Site	Parameter	Grazing management	
		Rotational	Continuous
Gantsi	Woody plants cover, %	35.9 ± 6.61	43.3 ± 11.24*
	Annual grass cover, %	5.3 ± 2.10	11.5 ± 3.02†
	Perennial grass cover, %	49.0 ± 5.81	27.1 ± 4.54†
	Total grass cover, %	51.8 ± 16.90	35 ± 11.62†
	‡Standing biomass, g^{-2}	41.7 ± 5.12	32.7 ± 6.60
	No. Species	10	12†
	Shannon diversity index, *H*	1.73	1.58
Hainaveld	Woody plants cover, %	37.9 ± 6.45	54.0 ± 11.9*
	Annual grass cover, %	4.08 ± 2.01	2.69 ± 1.23
	Perennial grass cover, %	27.5 ± 5.62	7.28 ± 1.21†
	Total grass cover, %	33.9 ± 6.12	8.83 ± 1.30†
	No. Species	10	10
	Shannon diversity index, *H*	1.29	0.5†

Note. Data are mean per plot and standard error.
* Statistically significant difference ($P < 0.10$).
† Statistically significant difference ($P < 0.05$).
‡ Standing biomass was not measured at Hainaveld ranches.

At the higher confidence level normally used for research (95%), woody vegetation differences between the ranches were not significant, but at the lower and acceptable confidence level associated with management decision-making (90%), there were more woody species on CG ranches at both sites. The aerial view of the Gantsi fenceline contrast also shows larger tree sizes on the CG and more grass cover on the RG grazed ranch (Fig. 2). An extended version of Table 1 showing test statistics is available in the supplemental material (http://dx.doi.org/10.1016/j.rala.2016.07.001).

Refer to Table 2 and Figure 3 for the effects of grazing management on individual grass species of different life forms and grazing value. Cover of high grazing value species was higher on RG than CG ranches at both sites. While cover of

Figure 2. An aerial photograph visualizing the difference in vegetation cover on adjacent ranches practicing continuous and rotational grazing in Gantsi district in western Botswana. (Photo Credits, Dudley Barnes).

Table 2. Cover of grass species of different grazing value on adjacent ranches grazed rotationally or continuously, in two districts of western Botswana

Site	Species	Grazing value*	Life form[†]	Cover, %	
				Rotational	Continuous
Gantsi	*Aristida congesta*	L	A	0	0.03 ± 0.02
	Aristida meridionalis	L	P	0	1.95 ± 1.19
	Brachiaria nigropedata	H	P	25.4 ± 5.98	1.22 ± 0.72[‡]
	Digitaria eriantha	H	P	1.64 ± 1.03	2.61 ± 1.52
	Digitaria sanguinalis	L	A	1.93 ± 1.23	4.62 ± 1.43
	Eragrostis lehmanniana	M	P	5.00 ± 1.35	3.72 ± 1.27
	Eragrostis pallens	L	P	1.38 ± 1.09	0.61 ± 0.61
	Eragrostis rigidior	M	P	4.60 ± 4.37	0.31 ± 0.31
	Melinis repens	M	A	2.21 ± 0.91	5.44 ± 1.51[‡]
	Schmidtia pappophoroides	H	P	2.33 ± 1.53	0.34 ± 0.31
	Stipagrostis uniplumis	M	P	6.32 ± 1.70	17.8 ± 4.89[‡]
	Urochloa trichopus	H	A	1.12 ± 0.79	1.53 ± 0.80[‡]
Hainaveld	*Aristida congesta*	L	A	0.24 ± 0.18	0.29 ± 0.18
	Dactyloctenium aegyptium	M	A	0.60 ± 0.60	0.08 ± 0.03
	Digitaria eriantha	H	P	11.69 ± 3.76	1.35 ± 0.55[‡]
	Eragrostis rigidior	M	P	11.39 ± 1.87	4.71 ± 1.33[‡]
	Melinis repens	M	A	1.38 ± 0.38	0.91 ± 0.31
	Pogonarthria fleckii	L	A	2.01 ± 1.73	0.06 ± 0.03
	Schmidtia pappophoroides	H	P	3.86 ± 0.94	0.35 ± 0.14[‡]
	Stipagrostis uniplumis	M	P	0.60 ± 0.28	0.86 ± 0.35
	Tragus racemosa	L	A	0.05 ± 0.03	0.01 ± 0.01
	Urochloa trichopus	H	A	1.80 ± 1.39	1.34 ± 0.46

Note. Data are mean per plot and standard error.

* L = low grazing value; M = medium grazing value; and H = high grazing value.

[†] A = annual; P = perennial.

[‡] Statistically significant difference ($P < 0.10$).

medium grazing value species was not different between RG and CG in Gantsi, it was higher on the RG than CG at Hainaveld. Black-footed grass (*Brachiaria nigropedata*), a high grazing value species, and silky bushman grass (*Stipagrostis uniplumis*), a medium grazing value species, dominated the RG and CG ranch, respectively. Cover of annuals, Natal redtop (*Melinis repens)* and crab finger grass (*Digitaria sanguinalis),* also a low grazing value species, were higher on the CG than RG ranch at Gantsi. Common finger grass (*Digitaria eriantha)* and sand quick (*Schmidtia pappophoroides*), all perennial species of high grazing value, and medium grazing value broad curly leaf (*Eragrostis rigidior*) were higher on the RG than the CG ranch at Hainaveld. A detailed version of Table 2 showing test statistics is available in the supplemental material (http://dx.doi.org/10.1016/j.rala.2016.07.001).

Implications for Grazing Management

In our two case studies, grazing practice changed grass cover and proportion of grass life forms and grazing value. The higher total and palatable perennial grass cover on RG compared with CG ranches, despite the high stocking rates in RG ranches, suggest the importance of recovery periods for grasses to recover nutrients lost to grazing in infertile soils and the benefits of high stocking rates to promote even grazing distribution. At high stocking rates, selectivity is reduced as grazing impacts are evenly distributed over the paddocks, hence both palatable and unpalatable species experience similar grazing levels.[3] However, under similar levels of defoliation, palatable grasses are more tolerant of defoliation than unpalatable grasses.[3,8] While the use of multi-paddock grazing with high stocking rates for short durations, such as

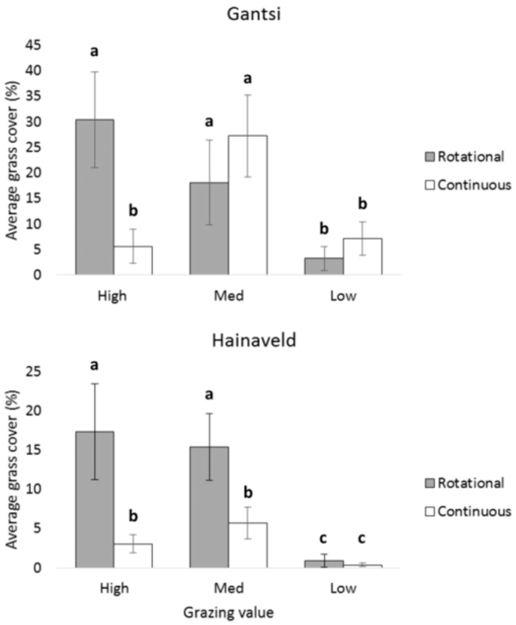

Figure 3. Mean cover (± SE) of grass species of different grazing values on adjacent ranches practicing continuous and rotational grazing in two districts of the Kalahari in western Botswana. Different letters indicate significant differences (Wilcoxons matched pairs test; $P < 0.05$).

the Gantsi RG improves forage resources, it may also be labor and cost intensive. Nonetheless, grazing management that uses few paddocks, such as the Hainaveld RG, may also improve forage resources with less intensive management.

As seen on CG ranches, low stocking rates are not sufficient to promote perennial grass establishment. This is because under CG at low stocking rates, cattle selectively graze the palatable species, which are not afforded adequate recovery, hence promoting uneven grazing distribution.[3,17,18] While continuous grazing at appropriate stocking rates appears to be sustainable in fertile environments,[6] on the infertile Kalahari sands, plant nutrient loss under grazing has much greater consequences for perennial grass persistence than in ecosystems with more fertile soils where nutrients are more easily replaced after removal in grazed tissue.[19] The grazed grasses in these infertile soils would be unable to adequately recover key growth-limiting nutrients such as nitrogen when continuously selectively grazed under a CG strategy. Therefore, while stocking rates form an integral part of grazing management, they must be applied together with management that supports uniform grazing and adequate recovery of the available forage to reduce overgrazing.

In addition to cover, grass species composition changed in response to grazing management. At Hainaveld, while species richness did not differ between grazing management, the diversity was higher on RG perhaps because of the abundance of few dominant species. Similarly, the higher number of species on the CG than the RG ranch at Gantsi suggests an increase of tail-end (minor unabundant) species that result from diminishing dominant species that are continuously selectively grazed.[20] Under appropriate grazing management that promotes uniform grazing and adequate recovery of grazed plants, minor species are out-competed by the dominants and make up a relatively small proportion of cover.[20] On the other hand, grass biomass (not measured at Hainaveld) including moribund material was not different between grazing management perhaps as a result of an accumulation of moribund material from the abundant silky bushman grass that was apparent under CG.

Apart from changes in grass dynamics, grazing management also changed woody vegetation cover. At the 90% confidence level, woody vegetation cover was higher on RG than CG suggesting that grazing management may have affected woody cover. Indeed, this would be expected seeing that continuous grazing has reduced grass cover, which may exert strong competitive effects on trees.[5]

To conclude, we provide a useful insight that grazing management that promotes even grazing distribution at appropriate stocking rates, and adequate recovery periods of grazed paddocks in the growing season, is important for maintaining the cover of palatable perennial grasses in semiarid rangelands. In sandy infertile soils, such grazing management is critical to allow recovery of nutrients lost to grazing and rebuilding of root biomass, which likely is more rapidly achieved in fertile soils. Thus, ranch managers and policy makers should not rely on changing stocking rates as a sole means of improving rangeland productivity and condition, especially in regions with sandy soils.

We recommend future research at larger spatial and temporal scales to determine long-term trends in vegetation responses to different grazing practices in the semiarid rangelands of Botswana. Long-term ranch-based research that combines rancher experience and scientific experiments to assess the effects of grazing management system on local rangelands is lacking.

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Appendix A. Supplementary Data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.rala.2016.07.001.

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Relevance of grazing research under global change - A review of drought and grazing studies in semi-arid rangelands

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Abstract

Global environmental change is increasingly recognized as a concern particularly in the marginal drylands where livelihoods hinge on rain-fed pastoralism. Current models predict increasing livestock numbers, shifts in amount, frequency and seasonality of rainfall, and an increase in frequency of extreme droughts – all of which are expected to have devastating effects particularly in Africa due to its vulnerability and low adaptive capacity. Thus, the aim of this review was to evaluate relevance of previous drought and grazing research with reference to content, applicability and methodological approaches to adequately address projected global changes in African dry rangelands. Our review found that, while grazing and drought research has become a large research focus globally, the African continent has been largely understudied, particularly with respect to empirical drought research. We also found that, although grazing-related research is well established and documented in Africa, it lacks certain levels of realism in terms of design and treatments. Moreover, experimental studies that evaluate combined effects of drought and grazing are lacking and this hampers our knowledge about African ecosystems' sensitivity to drought and grazing. We suggest robust multi-proxy experimental approaches to assess, simultaneously, the effects of drought and grazing, with possible adaptation strategies to global change.

Keywords: climate change, drought sensitivity, dryland ecosystems, multifactorial experiments, realism

Introduction

Global environmental change has become a central theme dominating contemporary discussions and research on human and policy dimensions. This is because environmental changes have potential threats to food security and human health due to their influence on food producing systems globally (Robinson, et al. 2011). Among the set of global environmental change drivers, climate and landuse change are arguably the two most fundamental ones, and have the potential to change ecosystem structure and function (MEA 2005, Reynolds, et al. 2007) depending on the intensity of the conditions and the resistance and resilience of the ecosystem (Hoover, et al. 2014). Effects of global change are predicted to be devastating particularly in the African continent due to its vulnerability and low adaptive capacity (Boko, et al. 2007).

In managed dryland ecosystems worldwide, changes in climate and landuse – usually assessed as changes in precipitation and grazing intensity, respectively – are the most important drivers of ecosystem change (D'Odorico, et al. 2013, Delgado-Baquerizo, et al. 2016). Livestock grazing is the most dominant landuse in these ecosystems where it provides livelihood security, be it on commercial scale or as subsistence practice (Martin, et al. 2016a, MEA 2005). It occurs in an estimated 25 to 50% of the world’s terrestrial area (Asner, et al. 2004, Havstad, et al. 2008). However, current global change models predict an increase in livestock numbers (MEA 2005, Reynolds, et al. 2010) as a result of growing human populations; particularly in Africa (Robinson, et al. 2011). Moreover, climate change models predict shifts in amount, frequency and seasonality of rainfall and an increase in frequency of extreme climatic events such as multi-year droughts (Cherwin and Knapp 2012, IPCC 2014, Knapp, et al. 2008). These extreme climatic events together with increasing livestock numbers may hamper dryland ecosystem functioning and service provision (Gaitán, et al. 2014, Ruppert, et al. 2015b).

In the light of these detrimental predictions, it should be scientific impetus to advance our understanding on how drylands will respond to future climate extremes and grazing scenarios, in order to invent sound mitigation strategies. A substantial amount of conventional research has focused on grazing strategies as management tools to avoid rangeland degradation and on vegetation responses to drought and grazing separately. However, in order to understand the potentially interactive effects of several global change drivers, the current gold standard is to simultaneously manipulate them in field experiments (Alba, et al. 2017, Power, et al. 2016). For this reason, this review evaluates relevance of previous grazing and drought research in semi-arid rangelands with the aim of identifying strengths, limitations and knowledge gaps in both content and approach with reference to the African continent. In addition, this study seeks to provide evidence for contemporary thinking and recognize advances made towards mitigation of predicted global environmental change impacts. Finally, recommendations for future experimental approaches are suggested.

Previous drought and grazing research

Grazing management strategies

Science-based grazing management, i.e. moving of animals across management units and/or landscapes in an effort to improve plant or animal performance, dates back as early as 1890s (Smith 1895). To date, grazing managers and rangeland scientists continue to report mixed results from ranch-scale grazing strategies and small-scale experimental studies (Teague and Barnes 2017). Two broad types of grazing strategies – continuous (CG) and rotational grazing (RG) have often been contrasted and compared (see Mudongo et al. 2016b for a detailed description of the grazing strategies).

Studies that compare grazing strategies are often inconsistent and have resulted in an unending debate on the superiority of either strategy. Most, but not all, grazing studies have concluded that RG is not superior to CG with respect to either range condition or animal performance (Briske, et al. 2008, Briske, et al. 2011, O'Reagain and Turner 1992). In particular, Briske et al, (2008) concluded that recommendations supporting the superiority of RG over CG are based on anecdotal rather than scientific evidence. However, a growing body of literature provides examples of scientific, case studies and individual rancher experiences where RG has out-performed CG with regard to both vegetation condition and animal performance at larger scales (Barnes and Hild 2013, Fynn, et al. 2017, Mudongo, et al. 2016b, Norton, et al. 2013, Odadi, et al. 2017, Steffens, et al. 2013, Teague and Barnes 2017, Teague, et al. 2013, Wolf 2016). These studies put more emphasis on adaptive grazing management that allows for uniform and sufficient grazing and recovery times and assessments of the grazing impacts at appropriate ranch-scales.

Several reasons have been given for the contradicting results of experimental research and ranch-scale experiences. One overarching reason is that the temporal and spatial scales at which grazing experiments (as reviewed by Briske et al. 2008) are conducted, are unrealistically short and small, respectively (Teague, et al. 2013).

Moreover, grazing experiments usually apply rigid treatments as compared to adaptive strategies, hence, obtaining results contrary to those from adaptively managed RG ranches (Teague and Barnes 2017). These authors further alluded that grazing experiments often lack to control for – or at least assess some key ecosystem drivers such as climate, management aspects (e.g. number of camps and stocking densities) and their interactions, and hence cannot easily be extrapolated to complex adaptive agroecosystems.

In a quantitative meta-analysis that included climate and management factors (number of paddocks, number of grazing days, size of grazing area and the experimental stocking rate) on the studies previously reviewed by Briske et al. (2008), Wolf (2016) discovered an increase in scale and an improvement in animal performance under RG. Furthermore, it is not easy to demonstrate the effects of grazing management from grazing experiments where animal movements are applied rigidly on small pastures that also lack plant species diversity (Barnes and Hild 2013). Moreover, the designs of many fixed RG systems continually rotates livestock through paddocks of either grown-out low quality (over-rested) or insufficiently rested grass – a system that is at odds with the natural movements of grazing herbivores (Fynn 2012, Steffens, et al. 2013). Thus, it appears that the outcomes of experimental grazing studies are rather influenced by the often-overlooked experimental designs and management (Teague and Barnes 2017).

While grazing management strategies (here: RG *vs.* CG) are already important in themselves for maintaining range condition and animal performance, their success also depends on stocking rates and its interplay with a given carrying capacity which is ultimately related to climatic, i.e. rainfall variability and amount. It is evident that stocking rate is an integral part of any grazing management strategy, where excessive stocking rates supersede management efforts (Briske, et al. 2008, Fynn, et al. 2017). Veld condition and carrying capacity is strongly affected by rainfall variability such that low rainfall or drought periods reduce carrying capacity (Fritz and Duncan 1994) calling for adjustment of stocking rates to conservative levels that do not compromise grazing plans (Fynn, et al. 2017). Despite a growing amount of literature showing examples where RG systems out-performed CG systems, up until now, there is substantial uncertainty surrounding generalizations of response patterns observed.

Grazing research – grazing or simulated grazing (clipping)

Grazing research has existed for many decades worldwide. This research ranges from small-scale clipping experiments studies (Dyer, et al. 1993, Hiernaux and Turner 1996, Mudongo, et al. 2016a, Turner, et al. 1993) to large-scale migratory ecosystems studies (Frank, et al. 1998, McNaughton 1979, 1985). Theoretical and empirical research in grasslands suggests that grazing may have positive (Frank, et al. 1998, McNaughton 1979), neutral (Knapp, et al. 2012) or deleterious effects (Belsky 1985) with respect to primary production. However, owing to their long evolutionary history with grazing herbivores, mesic grasslands have adapted well and often respond positively to grazing (Milchunas, et al. 1988, Milchunas and Lauenroth 1993). Thus positive response to grazing (also referred to as overcompensation), that is the capacity for regrowth to compensate for tissue loss (Augustine and McNaughton 1998, McNaughton 1983) often takes place in grasslands that have evolved with large herbivores and hence developed some tolerance to grazing (Del-Val and Crawley 2005, Milchunas, et al. 1988).

Apart from evolutionary grazing history, grazing effects may vary depending on the grazer i.e. generalist or specialist (Fynn 2012, Morris, et al. 1992), rate and intensity (Briske, et al. 2008), spatiotemporal scales (Frank, et al. 1998), prior rangeland condition (O'Connor, et al. 2001) and timing of grazing events (Mudongo, et al. 2016a). Nevertheless, studies of clipping experiments have shown that defoliation may increase current season productivity but reduces productivity significantly in the next season (Mudongo, et al. 2016a, Turner, et al. 1993). It is however acknowledged that, at high levels grazing generally reduces productivity irrespective of its temporal and spatial scales across landscapes.

Besides traditional ways of interpreting plant responses to grazing, there has been a shift towards a trait-based approach over the last decade (Diaz, et al. 2007, Linstädter, et al. 2014, Schellberg and Pontes 2012, Wesuls, et al. 2012). Plant functional traits help rangeland scientists to link plant morphological, physiological and phenological properties to their function in the ecosystem and hence can be useful indicators for rangeland condition (Schellberg and Pontes 2012). This is because it has been found that different species share traits that respond similarly to grazing disturbance (Jauffret and Lavorel

2003). Thus, Diaz and colleagues (2007) proposed a set of traits (e.g. growth form, life history – annual *vs*. perennial, plant height and architecture) that may be used to measure plant responses to grazing pressure. Although the use of functional traits has gained substantial support worldwide, it is still difficult to find consistent, and thus generalizable, trait responses that could serve as grazing indicators across dryland biomes (Diaz, et al. 2007, Linstädter, et al. 2014).

In a global meta-analysis study involving several plant traits,, Diaz et al (2007) found some inconsistent grazing responses across species growth forms (i.e. forb, graminoid, herbaceous legume or woody). For instance, forbs and woody species showed neutral responses to grazing whereas graminoids responded either neutrally or negatively to grazing (Diaz, et al. 2007). These response inconsistencies were linked to the broadness of the graminoid group in addition to a combination of precipitation and grazing histories.

Similarly, in a recent study in South African savanna and grassland biomes, Linstaedter et al. (2014) found no consistent trait responses to grazing across biomes, but only within a given biome, where some traits responded positively in the grassland and negatively in the savanna. These authors linked this finding to the convergent selective pressure of aridity and grazing (Quiroga, et al. 2010) and suggested that traits with opposite responses to grazing in the two biomes may have a unimodal response along a gradient of additive pressures of aridity and grazing. Furthermore, Wesuls and colleagues (2012) found no relationship between growth form and plant height with grazing pressure and also warned that traits that respond to grazing may vary under different habitat conditions and also depending upon prevailing climatic conditions. Thus, while certain key traits that may help rangeland scientists understand and predict grazing effects have been identified, their responses may be variable in different climatic and historical contexts of global drylands.

Drought research – natural occurring and experimentally imposed drought

Research on experimental drought has existed and advanced for at least more than two decades (Cherwin and Knapp 2012, Hoover, et al. 2014, Jentsch, et al. 2007, Knapp, et al. 2008, Lloret, et al. 2009, Tielbörger, et al. 2014). Findings of experimentally imposed droughts (Fay, et al. 2000, 2003, Grime, et al. 2008, Plaut, et al. 2012, Reichmann, et al. 2013) reiterate and support documented ecological responses to naturally occurring droughts (Copeland, et al. 2016, Knapp, et al. 2015, Tilman and El Haddi 1992, Zscheischler, et al. 2014). For this reason, experimental droughts that make use of total (Reynolds, et al. 1999) or passive rainout shelters (Yahdjian and Sala 2002) to study ecosystems sensitivity to drought have gained popularity worldwide. This is in the view that experimental droughts allow for stringent manipulation and/or control over other (confounding) environmental factors and hence disentangling drought effects from these (Hoover, et al. 2018).

Evidence from studies that suffered anecdotal, unplanned droughts suggests that drought may have long lasting ecological consequences particularly on primary production (Knapp, et al. 2015, Zscheischler, et al. 2014) and plant community composition (Tilman and El Haddi 1992). However, responses (as measured by primary productivity and community composition) from several drought sensitivity experiments have been variable (Byrne, et al. 2017, Mulhouse, et al. 2017, Sternberg, et al. 2017, Wilcox, et al. 2017). While Wilcox and colleagues (2017) found that aboveground net primary production was more sensitive to precipitation additions than reductions in drier ecosystems, Sternberg and colleagues (2017) found no precipitation legacies and negligible relationships with current season precipitation on peak biomass production in a Mediterranean grassland.

With respect to species composition in semiarid grasslands, Byrne and colleagues (2017) found neutral responses whereas Mulhouse and colleagues (2017) found a positive relationship between forb species richness and precipitation. The causes of variability have been attributed to local site differences related to soil properties and plant community composition (Hoover, et al. 2018) and lack of coordinated research approaches and defined metrics of drought sensitivity (Smith, et al. 2017). Thus far, patterns of ecosystem sensitivity to drought emerging from previous research are still largely ambiguous.

Limitations of previous research – the African context

Whereas grazing and drought research has become a large research focus globally, the African continent has been largely understudied, particularly with respect to drought research (Fig. 1). This hampers our knowledge about African ecosystems' sensitivity to combined effects of drought and grazing (Beier, et al. 2012, Hoover, et al. 2018). Of particular concern is the emerging evidence that the African continent is highly – potentially most – vulnerable to climate change (Boko, et al. 2007). In addition, drought experiments imposing long-term (>4 years) and/or extreme droughts (>50% precipitation reduction) as projected for African drylands (IPCC 2014) are lacking altogether.

Contrary to drought research, grazing-related research is well established and documented in African rangelands. However, several limitations surround interpretation and extrapolation of grazing experiments results. Similar to drought experiments, most grazing experiments lack realistic temporal and spatial scales and often do not make good representation of real world scenarios. Moreover, most grazing experiments are too artificial as they used simulated grazing by clipping vegetation. Clipping lacks realism as it does not include other characteristics of herbivory such as selective grazing (Morris, et al. 1992), hoof trampling and fertilization through dung and urine inputs (McNaughton 1983). Studies that attempted to account for other herbivory factors (such as trampling and dung addition) in clipping experiments are limited (e.g. Mudongo et al. 2016a).

Above all, short-term small scale grazing studies usually do not consider interactions with other elements of ecosystem function such as soil and climate properties, resulting in different and in most cases unsatisfactory outcomes when rigidly applied to larger scales (Teague, et al. 2013). Despite a growing body of knowledge, suggesting the importance of multi-discipline approaches (see section below) to study complex interactions in managed ecosystems (Flombaum, et al. 2017), studies that assess joint effects of drought and grazing are scarce. As a result, our understanding of the combined effects of drought and grazing in semiarid rangelands remains limited. Few studies have attempted to address these effects simultaneously, but they either used small-scale clipping experiments (Carlyle, et al. 2014, Koerner and Collins 2014, Zwicke, et al. 2013), mowing treatments (Vogel, et al. 2012) or grazing by sheep (Heitschmidt, et al. 2005). As already stated above, mowing or clipping lack critical levels of realism, whereas most of these studies were not located in Africa (although the study of Koerner and Collins included a site in Southern Africa) – where climate and evolutionary grazing histories are different.

Theoretical studies have also been used to explain the effects of aridity and grazing in drylands as convergent selective forces (Coughenour 1985, Milchunas, et al. 1988), but these original publications have not been sufficiently tested with empirical data. However, the convergence theory was confirmed in a field studies (Adler, et al. 2004) and a common garden experiment (Quiroga, et al. 2010). While these studies give relevant insights, they do not address the extremity of future climatic events as predicted by the global climate change models. Moreover, and similar to clipping experiments, common garden experiments using potted, isolated individuals are highly artificial as they neglect important community processes such as competition (and/or facilitation) and thus results need to be interpreted with caution and ideally should be repeated under more natural conditions.

In a recent study by Ruppert et al. (2015), a meta-analytical approach was used to evaluate combined effects of drought and grazing across drylands worldwide. Although meta-analyses provide invaluable insights that could not emerge from single studies, these approaches also have limitations or can potentially suffer from several caveats when not performed with extreme caution. It lies in the nature of things that meta-analyses lack control over the levels of the treatments tested; they have to make sense of those treatments and level of treatments that are available. In more general terms, meta-analyses may suffer from publication bias or the *file drawer problem* where important studies may be excluded. In addition, when performed carelessly, meta-analyses may also mix studies that used incompatible approaches (“comparing apples and oranges”) and thus result in possible wrong conclusions (Eysenck 1994).

Remote sensing and modelling techniques have also been used to estimate effects of rainfall variability and grazing in rangelands of southern Africa (Dube and Pickup 2001, Pickup 1996). Although these techniques provide good monitoring and early warning tools, they often need to be calibrated and validated with real field data. Besides, the usefulness of remote sensing data is limited in that specific vegetation responses such as shifts from perennial to annual herbage cannot be detected (see Dube and Pickup, 2001). Therefore, the lack of relevant drought experimental studies that include realistic grazing by large herbivores in southern African savannas do not only indicate presence of knowledge gaps in these grazed and drought-vulnerable regions, but also some limitations in international coordinated methodological approaches that allow comparisons of multi-site data that would improve understanding of these systems behaviour under global environmental change.

Combined effects of drought and grazing – the need for multifactorial experiments

Complex ecosystems such as dry rangelands require multifactorial studies in order understand the system behaviour and predict possible responses under projected environmental change. Empirical evidence suggests that grazing often interacts with other environmental factors such as climatic variability to give variable responses in community composition and productivity (Koerner, et al. 2014, Post and Pedersen 2008, Suttle, et al. 2007, Voigt, et al. 2007). These interactions may either amplify (Voigt, et al. 2007), mitigate (Post and Pedersen 2008) or reverse (Suttle, et al. 2007) climate change effects on trophic interactions, plant community composition, and several trophic levels, respectively. Koerner and colleagues (2014) also found that grazing interacted with increased rainfall variability to delay veld recovery.

Moreover, the strength and direction of interactive effects may even vary for different proxies of ecosystem performance (Guuroh, et al. 2018). For example, Guuroh and colleagues (2018) found that grazing reduced aboveground biomass but increased metabolizable energy. Altogether, the growing body of literature on combined effects of drought and grazing has underlined the complex nature of their interrelation and it is yet unclear whether these effects are simply additive or interactive (Ruppert, et al. 2015b, Zavaleta, et al. 2003).

The convergence theory (Coughenour 1985, Milchunas, et al. 1988) suggests that both aridity and grazing are convergent selective forces and thus select for similar if not identical plant traits. Experimental results supporting the convergence theory were reported elsewhere (Adler, et al. 2004, Quiroga, et al. 2010), although Adler et al. (2004) also indicated the importance of interactions of grazing history with edaphic factors such as soil texture in the selection of plant traits. Furthermore, in a global data integration study, Ruppert et al. (2015) found that drought and grazing may interact in complex ways depending on vegetation characteristics such as the predominant plant life history.

Thus, it is evident that grazed ecosystems are complex and hence their response to extreme climatic events (here: droughts) makes a strong case for experimental multifactorial studies that allow to assess effects of grazing and drought in isolation as well as in combination. In addition, effect strength and direction may be depended upon the assessed proxies of ecosystem performance (e.g. primary productivity, soil cover, plant functional traits, biodiversity), resting an additional case for the assessment of multiple ecosystem performance proxies within such multifactorial studies.

In order to measure individual and interactive effects of several global change drivers, the current contemporary approach is to simultaneously manipulate them in field experiments (Alba, et al. 2017, Power, et al. 2016). In this context, a rigorous and realistic experimental design is particularly important for understanding the response surface of ecosystem functions and services (Flombaum, et al. 2017, Knapp, et al. 2017), which is prerequisite for designing feasible adaptation strategies (Martin, et al. 2016b, Müller, et al. 2015).

Recommendations for future experimental approaches

As a way forward, and to contribute to a new generation of global change experiments, it is recommended that future global change researchers design large-scale multi-site field experiments that asses multiple determinants of ecosystem function and structure. Given the global nature of anthropogenic environmental change, ecological coordinated distributed experiments (CDE) that involve standardized and controlled protocols are needed to improve international collaborations and comparisons (Fraser, et al. 2013). These would help correct the problems of methodological differences associated with meta-analytical studies.

In a drought and grazing experiment for instance, the abiotic treatment (precipitation manipulation) should represent a centennial scale drought at that particular site and follow standardized protocols to make datasets comparable. In 2013 DroughtNet initiated the International Drought Experiments (IDE) with the aims of exploring terrestrial ecosystems' sensitivity to severe drought (DroughtNet 2015). According to the IDE, precipitation amount and pattern is manipulated in realistic ways through the use of rain interception shelters (Yahdjian and Sala 2002), based on a site's past climatic characteristics (Knapp, et al. 2017). In this way the experiment adds realism in terms of site-specific rainfall scenarios (Thompson, et al. 2013). Although the actual rainfall reductions differ across sites, the nature of the intended drought will be the same across all sites and thus keep the results more comparable than using a fixed rainfall reduction as done in the past.

As a result of the complexity of the combined effects of drought and grazing in drylands (Adler, et al. 2004, Ruppert, et al. 2015a), it is crucial that multiple factors need to be assessed simultaneously. In this context, edaphic factors should be included and evaluated to determine their influence on the dynamics of drought and grazing. Soil properties are important determinants of plant production in drylands (Archer and Smith 1972, Rezaei and Gilkes 2005). But they are often influenced by climate (Delgado-Baquerizo, et al. 2013) and disturbances such as grazing (Jing, et al. 2014, Yong-Zhong, et al. 2005), resulting in negative feedbacks on the resultant vegetation. Thus, in addition to the hypothesis of Milchunas et al (1988) as restated by Adler et al (2004), we propose addition of edaphic factors to the interactions of aridity and grazing (Fig. 2). We believe that edaphic factors play a very important role in determining vegetation productivity and vigour and hence grazing resistance traits.

For a biotic treatment, it is recommended that livestock be used to graze the experimental plots rather than simulated grazing. Using a factorial design, individual and combined effects of drought and large-herbivore grazing on ecosystems would be investigated. This approach brings novelty in the new generation of global change experiments, that go beyond respective climate change experiments by focusing on interactions of abiotic and biotic drivers (Power, et al. 2016).

Furthermore, in order to evaluate the ecosystem's sensitivity to drought (i.e. resistance and resilience to drought), a direct test of realistic management interventions through post-drought treatment changes is proposed. In a similar manner, grazing treatments may also be changed to mimic realistic grazing management scenarios under drought conditions such as resting / grazing during and after a drought to capture the grazing history effects hence assessing ecosystem recovery. However, to avoid tempering with the physical environment and creating an unwanted microclimate, particularly beneath the rainout shelters, it is imperative that controlled measurements of climatic factors that may influence plant growth dynamics (e.g. temperature, humidity, photosynthetic active radiation) and soil properties must be taken to separate artefact effects from treatment effects.

Thus the design of the rainout shelters should intercept rainfall while allowing free movement of grazing animals with minimum influence on the microhabitat. With this approach, multiple proxies of ecosystem performance such as aboveground net primary production, forage quantity and quality, soil properties and cover, community composition among others may be assessed. These kinds of multifactorial experiments may solve the problems associated with previous drought and grazing studies while at the same time bridging the knowledge gap and research imbalance. For the African continent and particularly savanna drylands of southern Africa where grazing-related land degradation is common, such an approach would help increase ecological understanding of grazed ecosystems under climate change.

Conclusions

Whereas grazing and drought research have become global research foci, it was apparent that the African continent is understudied particularly with respect to drought studies. Drought research is not only limited in terms of the number of studies, but also with respect to realistic site-specific drought intensities and extent of the drought treatments (i.e. the duration of drought). On one hand, grazing research is well established and documented in African rangelands, but grazing studies often lack realism with respect to temporal and spatial scale, nature of treatments (e.g. clipping *vs.* grazing), experimental designs (common garden *vs.* in-situ manipulations) and multifactorial approaches that include other elements of ecosystem function such as soil properties. This lack of realism was identified as one of the causes of inconsistencies in grazing research, what may partially explain the continuous debate on superiority of grazing systems.

However, we found few studies that used multifactorial approaches to study drought and grazing; either through theoretical analysis, meta-analysis, modelling and remote sensing, artificial grazing (clipping) or common garden experiments. As already mentioned, some of these studies lack realism and may need to be repeated or validated under more natural field conditions while some do not represent African rangelands due to different climate and evolutionary history of grazing. We further showed the need for rigorous and realistic multifactorial experimental designs that involve standardized and controlled protocols as well as site specific drought treatments, in order to bridge the knowledge gaps in African rangeland studies to overcome methodological problems associated with data integration and comparisons. Thus, present drought and grazing research and the state of knowledge does not adequately address future climate change scenarios predicted for southern Africa due to the limitations outlined above.

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Figure captions

Figure 5: Distribution of global coordinated drought experiments. The point indicates the location and size of the point indicates the number of experiments. Adopted from Hoover et al. (2018).

Figure 6: Proposed conceptual framework indicating the importance of edaphic properties (soil physical properties such as texture, and chemical properties such as carbon, nitrogen and phosphorus) on semiarid rangelands under climate change as per the convergence model. Modified from Adler et al. (2004).

Appendices

Appendix S3.1

Table A3.1: Grazing plan at DroughtAct camp

Year	Growing season								Dry season												Growing season			
	Jan		Feb		Mar		Apr		May		Jun		Jul		Aug		Sep		Oct		Nov		Dec	
2014	🟩	🟩	🟨	🟨	🟨	🟩	🟩	🟨	🟨	🟨	🟨	🟨	🟩	🟨	🟨	🟨	🟨	🟨	🟩	🟨	🟨	🟨	🟨	🟨
2015	🟩	🟩	🟨	🟨	🟨	🟩	🟩	🟨	🟨	🟨	🟨	🟨	🟩	🟨	🟨	🟨	🟨	🟨	🟩	🟨	🟨	🟨	🟨	🟨
2016	🟩	🟩	🟨	🟨	🟨	🟩	🟩	🟨	🟨	🟨	🟨	🟨	🟩	🟨	🟨	🟨	🟨	🟨	🟩	🟨	🟨	🟨	🟨	🟨
2017	🟨	🟩	🟩	🟨	🟨	🟨	🟩	🟩	🟨	🟨	🟨	🟨	🟩	🟨	🟨	🟨	🟨	🟨	🟩	🟨	🟨	🟨	🟨	🟨

Key

🟩 Grazing by 25 – 30 herd of cattle

🟨 Resting

Appendix S3.2

Table A3.2: Classification of drought intensity via the standardized precipitation index (SPI) used in the DroughtAct experiment as adapted from the National Drought Mitigation Centre of the USA (http://droughtmonitor.unl.edu/classify.htm).

SPI Class	Description	Possible impacts on primary production of rangelands	SPI values
0	Normal	-	+0.5 ≤ SPI ≥ -0.5
1	Abnormally Dry	Going into drought: short-term dryness slowing growth of vegetation	-0.5 < SPI > -0.8
2	Moderate Drought	Some damage to vegetation	-0.8 ≤ SPI > -1.3
3	Severe Drought	Production losses likely	-1.3 ≤ SPI > -1.6
4	Extreme Drought	Major production losses	-1.6 ≤ SPI > -2.0
5	Exceptional Drought	Exceptional and widespread production losses	-2.0 ≤ SPI

Appendix S3.3

Table A3.3: Results of repeated measures ANOVA (Type II) testing the effect of block on soil moisture at seven depths at the DroughtAct experiment measured before treatment implementation from December 2013 to May 2014.

Depth (cm)	Source	Df	*Chisq*	*P*
10	Date	28	23280.6	***
	Block	3	14.3	**
20	Date	28	12967.0	***
	Block	3	15.5	**
30	Date	28	11048.6	***
	Block	3	8.2	*
40	Date	28	6441.7	***
	Block	2	1.6	0.449
50	Date	28	3635.3	***
	Block	2	3.7	0.160
60	Date	28	2739.4	***
	Block	2	2.8	0.246
70	Date	28	3355.3	***
	Block	1	2.7	0.098

*< 0.05, ** < 0.01, *** < 0.001.

Appendix S3.4

Table A3.4: ANOVA results testing the main effect of block on different topsoil (0 – 10 cm) properties at the DroughtAct experiment measured before treatment implementation in September 2014.

Response variable	**Df**	***F* value**	***P* value**
pH (H_20)	3	3.22	*
P	3	0.41	0.75
Total N	3	3.26	*
Total C	3	0.48	0.70
CEC	3	0.85	0.48
Cu	3	1.00	0.41
Mn	3	0.24	0.87
Fe	3	2.26	0.10
Zn	3	3.68	*
Clay	3	1.39	0.27
Silt	3	2.51	0.07
Sand	3	2.83	0.06
Bulk density	3		

*< 0.05, ** < 0.01, *** < 0.001.

Appendix S5.1

Table A5.1: ANOVA tables for response of Brachiaria nigropedata to first and second season clipping

B. nigropedata						
	Season 1			Season 2		
Response: Productivity						
Source	Df	*F*	*P*	Df	*F*	*P*
Treatment	3	3.11	0.01	5	8.19	<0.001
Initial tuft area	1	5.34	0.01	1	3.81	NS
Treatment x Initial tuft area	3	2.42	NS	5	1.31	NS
S. uniplumis						
Treatment	5	3.78	0.001	5	19.2	<0.001
Initial tuft area	1	21.8	<0.001	1	1.89	NS
Treatment x Initial tuft area	5	2.43	0.01	5	0.49	NS