

**Changes in species composition, herbaceous biomass yield, soil seedbank
and soil properties of semi-arid grassland subjected to different levels of
rainfall interception and resting period**

By

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Declaration

I, **Thabo Patrick Magandana**, declare that the thesis which I hereby submit for the degree of Doctor of Philosophy in Animal Production Management at the University of Pretoria, is my own work and has not been previously submitted by me or anyone for the degree at this or any other tertiary institution.

Date-----

Signature-----

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Dedication

In loving memory of my late grandparents

Dedicated to:

My mother, Nofezile Magandana

My father, Roy Rooi Magandana

My beloved partner, Ms Noluvo Mfeketo

My sons, Bulumko and Azabeluncedo Magandana

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List of acronyms and initialisms

ANOVA: analysis of variance
ANPP: aboveground net primary productivity
ARC: Agricultural Research Council
C: carbon
Ca: calcium
Ca: calcium
Cl: chlorine
EC: electrical conductivity
GHG; greenhouse gases
GLM: general linear model
K: potassium
kg: kilogram
Mg: magnesium
mg: milligram
mL: millilitre
N: nitrogen
Na: sodium
NO₂: nitrite
NO₃: nitrate
P: phosphorus
PCA: principal component analysis
Proc: procedure
RI: rainfall interception
RP: resting period
RUE: rain-use efficiency
SANBI: South African National Biodiversity Institute
SAS: Statistical Analysis Systems
SO₄: sulphate
SWC: soil water content

Changes in species composition, herbaceous biomass yield, soil seedbank and soil properties of semi-arid grassland subjected to different levels of rainfall interception and resting period

Abstract

Climate change is expected to result in rainfall reduction in South African semi-arid and arid rangelands and may have severe ecological consequences. This rainfall reduction may cause irreversible and substantial socio-economic changes if resilient based management strategies are not developed to assist farm managers in their ability to sustain desirable ecosystem services by incorporating adaptive management strategies. Therefore, it is important to understand how these rangelands will respond to predicted impacts of climate in particular that of rainfall reduction. The current study was conducted to determine the impact of rainfall interception on soil water content and soil properties, annual primary production vegetation composition and soil seedbank storage. To achieve this, rainout shelters that reduced rainfall at several levels (15%, 30% and 60%) and ambient rainfall (0%) interceptions were used. Effects of resting periods (70 and 90 days) were investigated (following simulated grazing) with the rainfall interception treatment to determine the main effect and its interaction with these treatments. The data were collected over three seasons (with the exception of winter) in 2016/17 and 2017/18 and used in four separate studies. In the first study, the effects of rainfall interception and resting period on residual soil water content and selected soil chemical properties of the semi-arid grassland were evaluated. Results from this study showed that reducing annual rainfall by 60% could negatively affect residual soil water content, thus influencing regrowth potential after defoliation by grazing or cutting natural grasslands. The negative effect of rainfall interception on residual soil water content was higher during summer than autumn. Rainfall interception led to higher extractable residual soil cations (calcium, potassium, magnesium, sodium, and phosphorus) and anions (sulphate and nitrate) partly because of the interception in leaching and partly owing to reduced uptake of soil nutrients by plants. Rainfall interception, however, did not significantly affect soil pH, total N, and total C, indicating the minimal impact of climate change manifested in terms of rainfall interception on these parameters. Generally residual soil water content was higher at a deeper soil layer than the top layer, suggesting that plants with creeping ground cover and tap root systems would have competitive advantage to dominate the vegetation at 15% and 60% rainfall interception (RI), which was characterized by low residual soil water content, rather than 0% or 30% RI.

Under 60% RI scenarios, however, the plants might not be able to grow fast and switch to reproductive stage.

In the second study annual net primary productivity (ANPP) was evaluated of various functional groups as affected by different intensities of rainfall interception in the semi-arid grasslands of the province of Gauteng in South Africa. It was concluded that reduced rainfall had a significant negative impact on ANPP at 60%. Reduced rainfall significantly ($p = 0.0188$) affected grass ANPP more than forbs ANPP. Whereas grass ANPP decreased with the reduction in rainfall from 2017 to 2018, that of forbs increased. Various grass species responded in different ways to the reduced water supply, because those tropical grass species that were equipped with better ability to fix carbon dioxide by closing their stomata were likely to be affected less by rainfall interception than temperate and other tropical grass species adapted to waterlogged areas. It was found that grass species such as *Eragrostis curvula* required less water to produce herbage than *Digitaria eriantha*. Livestock farmers who rely on natural grazing land should promote the growth of grasses such as *E. curvula* to produce enough grass during periods of low to moderate intensity rainfall interception, because such grass species are more favourable to those conditions and able to produce more biomass per unit of rainfall. This can be achieved by reseeding the rangelands with such grass species.

In the third and fourth study, seasonal herbaceous structure and the response of biomass production to rainfall interception and resting period were studied. In this study, it was concluded that rainfall interception associated with climate change posed a threat to the country's rangeland productivity as it would lead to a decreased forage biomass yield. It was found that increaser grasses and forbs dominated under high rainfall interceptions. Although the grassland productivity had shown resilience to a small interception in rainfall (up to 15%), a severe reduction would lead to changes in the herbaceous layer, which might lead to rangelands being dominated by forbs rather than grasses beyond a 30% interception in rainfall. Within the grass species, increasers are more tolerant of rainfall interception than decreasers, and thus are likely to increase with the decrease in rainfall beyond 15%. Resting the rangelands for 90 days or more compared with 70 days would improve rangeland biomass productivity during spring and summer, whereas there was no benefit to resting for 90 days compared with 70 days during the autumn harvest. Further studies need to be conducted to quantify the impact of long-term rainfall interception on the growth pattern of key species, soil vegetation cover, soil nitrogen and carbon dynamics, soils seedbank and soil microbiota diversity to accurately

model and predict the impact of reduced rainfall on the country's rangelands to come up with climate change adaptation strategies.

Finally, in the fifth study, the effects of rainfall interception and resting period on soil seed banks (SSBs), were determined. The results showed that rainfall interception had a negative effect on a grass SSB, whereas it improved the forb SSB. Rainfall interception affected the SSB of the most palatable species such as *Themeda triandra* and *D. eriantha* negatively. These species were fewer in the SSB compared at 60% RI, because they did not produce seed. Therefore rainfall interception might lead to grasslands being dominated by forbs, resulting in larger bare patches that expose the land to degradation through soil erosion. Forbs seemed to be suppressed by grasses at lower rainfall interception treatments. However, the authors recommend that more studies of this nature should be conducted, taking into consideration the effect of time lags between SSB collections. This calls for alternative interventions that could be considered if the droughts became more persistent, for example reseeded of rangelands with naturally occurring grasses in a specific area for example *E. curvula*.

Key words: decreaser, increaser, forbs, rainfall reduction, resting period

General introduction

Background and rationale

Over 40% of the earth's land area is characterized as rangelands (McCollum *et al.* 2017). These rangelands are distinguished by native plant communities that are associated with domestic grazing and wildlife animals, and managed by ecological methods rather than agronomic ones (Society for Range Management 2014). It is generally agreed that climatic changes affect and change rangeland ecosystem processes and functions (Polley *et al.* 2013; McCollum *et al.* 2017). However, there is uncertainty with regard to spatial variations in the rates of rainfall change and temperature (Christensen *et al.* 2007). Furthermore, the degree to which climate change will affect the rangelands would vary from region to region (Briske *et al.* 2015). One of the ways in which rangeland managers on all scales could deal with climate change uncertainty is through building adaptation strategies (Marshall & Smajgl 2013). The results of scientific experiments that tested the effects of climate change and predictions through modelling could be used to improve and plan the management of rangelands (Walters & Holling 1990). These studies would allow managers to potentially detect and correct the negative effects of climate change before serious irreversible damage occurs (McCollum *et al.* 2017). This would help communities with the identification of appropriate strategies to manage rangelands during climate change scenarios (Moir & Block 2001).

Droughts occur frequently in South African semi-arid and arid rangelands and may have severe economic and ecological consequences (Vogel 1994). Although the effects of drought might be short term when it is followed by recovery in subsequent years with higher rainfall (Ellis & Swift 1988), sometimes prolonged droughts trigger substantial and irreversible socio-economic changes (Vetter 2009). Rangeland managers should adopt resilience-based management strategies to assist them to plan and incorporate adaptive management practices to sustain desirable ecosystem services in an uncertain and changing climate (Briske *et al.* 2008). To achieve this, it is of paramount importance to consider ways in which ecosystems may cope with the effects of the climate change (Martine & Guzman 2002). Therefore, this study is conducted to investigate these effects of climate change. Consequences of climate change such as hazards and disturbances may lead to behavioural responses of plants, which may result in secondary impacts (Kasperson *et al.* 1988). These behavioural responses include the growth forms such as creeping growth form as opposed to tufted growth form. In turn, these secondary effects may have long-lasting adverse effects (Peters *et al.* 2007).

According to Martine and Guzman (2002), socio-economic factors such as poverty and loss of economic activities following disasters and factors such as inappropriate land use, soil erosion and deforestation exacerbate climate change effect on the rangeland ecosystems functions and processes (Martine & Guzman 2002). Climate change and variability expressed through drought pose the greatest threats to African countries, because of their generally low adaptive capacity, lack of safety nets in the form of supplementary feeds and high rates of poverty (Thomas & Twyman 2005). Drought conditions associated with climate change can adversely affect the agricultural industry owing to water scarcity (Sharma & Gobi 2016). Droughts are projected to occur more frequently in semi-arid and arid areas as a consequence of global warming because of low and unpredictable rainfall, (IPCC 2007).

Rain-fed agriculture is already threatened by droughts in southern African countries such as Zimbabwe, which are experiencing it during the growing season (Cooper *et al.* 2008; Mupangwa *et al.* 2011). Apart from its key role in photosynthesis, water is the transport medium for nutrients from the soil to the plant. Hence the impact of climate change, expressed in terms of low rainfall, is detrimental to the whole ecosystem. Apart from rainfall the other important factor is resting the field as this allows new seedlings to grow. The grasses also get a chance to shed seeds for the soil seed bank reserves. This will prevent land degradation as a result of overgrazing and continuous grazing.

Problem statement

South African farmers rely mainly on the rain-fed natural rangelands for all-year-round grazing of their animals. However, rainfall interception and continuous grazing which is mainly practiced in communal rangelands may limit the availability of forages for the grazing animals. Parts of South Africa are currently facing reduced rainfall because of climate change effects, and this has a negative impact on agriculture. In addition to recurrent drought, which has been happening for the past few years, some grasslands are being encroached by invading shrubs, woody plant and undesirable grass species that are annuals or weak perennials. Bare patches and eroded areas also expand as a result of this recurring drought. It is argued that these forbs are relatively drought tolerant and less palatable to grazing animals, which may reduce carrying capacity of the veld. There are few studies that have investigated the effect of reduced rainfall and resting period on productivity, species composition of herbaceous and soil layer. Moreover,

climate change and drought make it difficult for farmers to cope with having less forage available for their animals. Some farmers sell their animals, whereas other animals die of starvation. The summer-rainfall native rangelands of South Africa have poor nutrient status with low crude protein content, which is below the required level (7%) to fulfil maintenance requirements (Keba *et al.* 2013). This results in low rumen microbial activity in animals, which leads to poor digestibility of the feed material (Hariadi & Santoso 2010). The major challenges for smallholder farmers and the reason for poor livestock performance are associated with poor feed quality as they depend solely on natural rangelands (Ogunbosoye & Babayemi 2010).

Aim

The overall aim of this study was to quantify the impact of climate change, manifested mainly in the form of reduced rainfall and resting periods, on species composition, soil seed bank, forage production and condition of semi-arid grasslands in South Africa.

Outline of the study

The components of this PhD study are outlined as follows. In chapter 1, a detailed literature review on rangelands is presented. A brief overview of South African rangelands is followed by a discussion of rainfall effects on soil, rangeland soil seed bank productivity and species composition. The chapter provides information about the impact of global warming on South African climate and the direct and indirect influences of these changes on rangeland production. Chapter 2 investigates the effect of climate change expressed through rainfall interception and resting period on soil residual water content and soil cations (calcium, magnesium, potassium and sodium). Chapter 3 focuses on the impact that simulated climate change, expressed through reduced rainfall, has on rangeland vegetation annual net primary productivity in semi-arid South Africa. Chapter 4 examines the effects of simulated rainfall interception/drought and resting periods on the composition of the herbaceous species vegetation and aboveground biomass production in semi-arid areas of South Africa. Chapter 5 examines the impact of simulated climate change expressed through rainfall interception and resting periods (70 and 90 days) on the soil seed banks of rangelands in semi-arid regions of South Africa. Chapter 6 presents a summary of the findings, conclusions and recommendations for future research.

The thesis is presented in chapter format, each chapter having an Introduction, Materials and Methods, Results and Discussion, and Conclusion. Two chapters (Chapters 3 and 4) were published in peer-reviewed ISI-rated Agronomy (Multidisciplinary Digital Publishing Institute). [DOI: 10.3390/agronomy10111807; DOI: 10.3390/agronomy11040730].

Chapter 1

Literature review

1.1 Brief overview of rangelands in South Africa

Rangelands may be defined as the land in which the native vegetation is dominated by grasses, trees, shrubs and grass-like plants (Allen *et al.* 2011). The vegetation is further classified into biomes according to the type that occurs in a particular area. One of these biomes is grassland, which represents about 26% of the world land areas and 70% of the agricultural land areas. About 20% of the world's carbon and nitrogen stocks are contained in the grassland biome (FAO 2009). However, these grasslands are being threatened by challenges such as land degradation and climate change, which are considered difficult to evaluate (Thompson *et al.* 2009). These rangelands are a source of feed for livestock and wildlife.

Approximately 90% of South Africa is sub-humid or semi-arid and about 10% is considered hyper-arid (Schulze 2008). Only 14% of the country is arable, with one fifth of that land having high agricultural potential (DEA 2011). Globally the impacts of climate change on rangelands have been reviewed extensively. However, the emphasis has been on temperate North American and European rangeland systems (Campbell *et al.* 2000; Nosberger *et al.* 2000; Polley *et al.* 2000; Hopkins & Del Prado 2006; Baron & Belanger 2007). Therefore, strategies to address these changes were discussed in the European context. Moreover, because South Africa supports a two-tiered agricultural system of commercial and communal farmers, the agricultural sector experiences a range of vulnerabilities (DEA 2013).

Climate is one of the factors that is responsible for a shift in the regional vegetation (Lei & Middleton 2018) across regions. A relict status of some species may occur as a result of drought (Middleton & Souter 2016). Seeds in the soil seed bank do not diminish immediately after drought, but density and species richness decrease over time (Brock 2011). The potential resistance of South African grasslands to reduced rainfall is unknown. However, it is vital to understand the response of grassland species to the threat climate change causes on the soil seed bank.

Rainfall interception is also expected to have an impact on the soil water content. This soil water content is responsible for various processes in the soil, which include diffusion and nutrient availability (Zhang *et al.* 2014).

Therefore, there is a need to explore these climatic impacts on rangeland productivity and produce strategies that can be used to overcome the negative influence of climate change in the South African context.

1.2. Impacts of rainfall on rangeland ecosystem

1.2.1. Impacts of rainfall on soil productivity

Soil provides its ecosystem with elements such as carbon (C) and nitrogen (N) that are important for plant growth and sustainable food production (De Vries *et al.* 2012). Soil C and N cycling across different climate zones is affected indirectly by rainfall (Fay *et al.* 2011) owing to their influence on root biomass and aboveground productivity (Wang *et al.* 2014). Studies that were conducted on the effects of drought and rewetting argued that rewetting and drought can kill soil microbes, plants, soil fauna and disrupt soil structure, leading to a pulse of C and N mineralization and consequently increased loss of N and C from the soil (Liiri *et al.* 2002; De Vries *et al.* 2012). Soil food web is important in the C and N cycling process and the legacy impacts may weaken the supply of ecosystem services long after the drought has ended (De Vries *et al.* 2012). Regions with increasing annual rainfall may also be affected by increasing evapotranspiration as a result of increased temperatures and this could constrain soil water availability during the growing season. Nutrient availability, biogeochemical processes, gaseous and leaching losses may be affected negatively in the long run for C and N pools in soil (Matzner & Borken 2008).

Soil C and N stocks are expected to be low in arid lands because of low rainfall that limits biomass production (Du Preez *et al.* 2011). Higher decomposition rates of dead material because of increased temperatures and lower rainfall may contribute to losses of C through oxidation and N through ammonia volatilization (Kotzé *et al.* 2013). Soil N could also be leached to deeper soil profiles under heavy rainfall, and other plant nutrients could be exposed to erosion, depending on the soil texture, and this could affect the distribution of nutrients in the plant-soil system (Schuman *et al.* 1999). Soil chemical properties and nutrient mineralization are affected by processes that depend on temperature (Liebig *et al.* 2006).

Rainfall reduction as a result of climate change limits resource availability as the low soil moisture levels reduce diffusion (Naylor & Coleman-Derr 2017). Although some studies found no significant effect of reduced rainfall on soil nitrogen content (Sardans *et al.* 2008a;

Xiang *et al.* 2008), others found significant increases in ammonium nitrogen levels (Blackwell *et al.* 2013).

1.2.2 Effect of precipitation and resting period on the soil seed bank

Ecosystems across the world are affected by diverse impacts of climate change. Climate change will also affect the soil seed bank as it is determined by the plants that are above the ground. A soil seed bank is a repository for the next generation of plants. These are the seeds on the soil surface and within the soil (Hu *et al.* 2019). The soil seed bank is important in grassland productivity as it is the basis of survival, population settlement, expansion and reproduction (Milberg & Hansson 1993). The history and the current situation of a community is reflected in the soil seedbank (Thompson 2000; Kalamees *et al.* 2012). Any factors contributing to vegetation productivity or reduction in biodiversity and grassland degradation can affect the size and the composition of the soil seed bank (Dreber & Esler 2011; Báldi *et al.* 2013). The distribution of rainfall also affects seed production and release (Guttermann 2012). Disturbance related to environmental changes influences the overall heterogeneity in the soil seed bank (SSB) (Solomon *et al.* 2006; Kassahun *et al.* 2009).

By allowing a portion of their offspring into dormancy and therefore forming a seed bank, plants commonly delay reproduction (Baskin & Baskin 1998). A reduced mean annual number of offspring is a result of delayed reproduction, which is an apparent maladministration (Aikio *et al.* 2002). A soil seed bank is an important aspect of grassland as it determines its current and future condition. Seed recruitment from the seed bank is restricted to soil parameters and periods with favourable conditions for seed germination (Solomon *et al.* 2006). Soil water is one of these important variables (Snyman 2004), together with soil pH (Henig-Server *et al.* 1996), light (Trabaud & Renard 1999) and heat exposure (Snyman 2005b).

Simulated climate experiments provide the best approach to studying the processes that determine community changes at stand level (Del Cacho *et al.* 2012). Most farmers rely on the natural rangeland for all-year-round grazing of their livestock and therefore the status of the soil seed bank is important to understanding how climate change will affect it and prepare for the future. This will also assist the farmers to understand the measures that can be undertaken to restore the rangeland. Understanding the deterioration of the rangelands will also assist in the ways in which they can be restored (Solomon *et al.* 2006). Climate manipulation may affect the soil seed bank when the seed input is not depleted by the germination owing to unfavourable

conditions imposed by climate modification (de Cacho *et al.* 2012). Grassland researchers and scientists predict a reduction in cover and productivity because of summer droughts (Hufkens *et al.* 2016; Basto *et al.* 2018). However, some studies on climate manipulations show that these responses will differ from community to community and soil properties (Fridley *et al.* 2011).

1.2.3. Effect of precipitation on annual net primary production

Net primary production (NPP) is sensitive to soil water availability and is the net amount of carbon removed by plants from the atmosphere (Byrne *et al.* 2013). In applied and basic ecology measuring, aboveground net primary production (ANPP) is a frequent goal as it gives the trophic and carbon balance interactions (Byrne *et al.* 2013). In the rangeland perspective, this ANPP is used to estimate the available forage and to determine stocking rates for managed wildlife and livestock. High forage production and dominance of highly acceptable grass species are indication of a rangeland in good condition (Sisay & Baars 2002). Aboveground net primary production is influenced by factors such as soil nutrients, rainfall and grazing management. However, rainfall is very much linked to ANPP in grassland biomes (Sala *et al.* 1988). Aboveground net primary production is expected to respond to soil water changes owing to variability in rainfall (Byrne *et al.* 2013). Predictions of drought have triggered the need to conduct field experiments that involve interception of rainfall to understand the effect of drought on grassland production (Chen *et al.* 2012; Byrne *et al.* 2013).

There is a relationship between NPP, nutrient cycling, secondary productivity and animal biomass (McNaughton *et al.* 1989). Rainfall and evapotranspiration account for a large portion of ANPP in grasslands (Sala *et al.* 1988). Plant production rates increase with a rise in annual rainfall on a regional to continental scale (Epstein *et al.* 2002) and this leads to grassland biodiversity (Khumalo *et al.* 2012). Availability of water is the most important factor that regulates biological activities in arid land ecosystems (Baez *et al.* 2013). The NPP responds more strongly to increased rainfall in arid and semi-arid ecosystems than to drought, because those plants are adapted to tolerate or avoid drought (Knapp & Smith 2001). The response of NPP to altered rainfall also depends on plant community structure, functional diversity and species composition (Collins *et al.* 2008; Baez *et al.* 2013).

1.2.4. Effect of precipitation on species composition

The species composition is important in assessment of rangeland condition as the variability in grass species affects acceptability and palatability to herbivores (Solomon *et al.* 2007). Rainfall plays an important role in determining species composition in rangelands (Launghlin & Abella 2007). In the grassland biome, rainfall can act as an ecological filter that controls species composition and diversity (Baez *et al.* 2013). In this changing climate, plant functional diversity and species composition are vital to maintain processes such as NPP (Chapin *et al.* 1997). Therefore it is of paramount importance to understand how plant species respond to chronic drought or increased annual rainfall (Baez *et al.* 2013).

The response of species to drought can be observed through plant functional traits such as perennials or annuals, plants with high photosynthetic rates per unit of nitrogen C₄ or low photosynthetic rates per unit of nitrogen (C₃) grasses or forbs (Schmitt & Edwards 1981; Knapp *et al.* 2002), which are good indicators of whether the rangeland is in a good or bad condition. Plant functional diversity and species composition are important in maintaining processes such as NPP in the current changing climate (Chapin *et al.* 1997; Tilman 1999). Altered rainfall predictions and their impact on arid ecosystems require a good understanding of how the species and plant community structure will respond to drought as a result of reduced annual rainfall. Previous studies on long-term effects of manipulated rainfall have shown unexpected and non-linear responses in plant functional diversity and community (Harpole *et al.* 2007; Suttle *et al.* 2007). In arid ecosystems, grasslands are changing from being dominated by C₄ grasses to being dominated by C₃ shrubs (Van Auken 2009). Mean annual rainfall in particular affects functional trait diversity, net primary production and species composition in grassland ecosystems (Sala *et al.* 1988; Huxman *et al.* 2004).

Therefore, it is important to understand how the variability in rainfall affects the ecosystem and these transitions are important in predicting large-scale changes in shrub and grass species richness under future climate scenarios (Baez *et al.* 2013). The dynamics of the dominant grass species largely determine the changes in vegetation community and its resistance to drought (Evans *et al.* 2011).

1.3. Global warming and its effect on climatic conditions in South Africa

In South Africa the effects of global warming on climate change are showing increasingly. According to DEA (2017) unless radical action is taken to reduce greenhouse gas emissions (GHG), temperatures are expected to rise by more than 4 °C over the southern African interior by 2100 and by more than 6°C over the northern, western and central parts of South Africa. Examples of extreme weather events that are noticeable in South Africa to date include wild fires as a result of drought in the Western Cape, drying of dams in the Eastern Cape, and rises in vector and waterborne diseases (Chersich & Wright 2019).

These include malaria, which is transferred by mosquitos, Rift Valley fever and other diarrhoeal pathogens (Chersich & Wright 2019). Most climate scientists agree that global warming will be caused by the build-up of GHG in the atmosphere and will lead to political, environmental and socioeconomic implications at regional, national and global level (Oroud 2018). The impact of global warming on rainfall levels will vary from region to region. There has been concern that variability in climate could lead to climate sensible impediments in developing countries (IPCC 2007). Apart from expected increases in temperatures because of global warming, global change models forecast more severe extreme and frequent events such as heat waves, floods and drought (Feller & Vaseva 2014). Such climatic extremes that occur regionally (Gilgen & Buchmann 2009) are economically and ecologically relevant to forestry and agriculture (Nair 2014).

Plant species and varieties react differently to these regional abiotic stresses (Wishart *et al.* 2014). The availability of water is one of the major limitations on plant productivity worldwide (Gilgen & Buchman 2009). The aboveground net primary productivity (ANPP) depends mainly on mean annual rainfall (Knapp & Smith 2001). The ANPP increases with annual rainfall quantity (Sala *et al.* 1988), and grass species composition shifts from short grass in low rainfall areas to tall grass in high rainfall areas (Küchler 1974). High rates of water loss as a result of high atmospheric vapour pressure deficit or from drying soil and low rainfall inputs may lead to water stress for plants (Gilgen & Buchman 2009).

These events may increase with the predicted global warming as the water deficit is forecast to increase in certain regions as a result of climate change. Comparable patterns of rainfall, productivity and composition occur across rainfall gradients in grassland regions worldwide (Fay *et al.* 2002). Climate change models predict that warming and other elements

of climate change scenarios will be accompanied by altered rainfall patterns (Easterling *et al.* 2000). The altered distribution and decrease in rainfall could result in dry intervals and lower soil water content availability (Watson *et al.* 1997). Deposition of some elements such as sulphur and nitrogen may be increased or decreased by climate change depending on the direction and precipitation volume (Langner *et al.* 2005; Hole & Engardt 2008).

1.3.1. Precipitation

Transpiration and evapotranspiration are among many climatic factors that are direct indicators of water regime from regional to global scale and are also used as climate change indicators (Fu & Feng 2014). Climate change alters precipitation patterns by increasing frequency and intensity of precipitation events especially in summer (Lim *et al.* 2020). Most climate models have found a seasonal cycle of precipitation over Africa (Dunning *et al.* 2016). The increased atmospheric water vapour in a warming climate leads to a complex pattern of change in tropical rainfall, with rainfall amount changing seasonally (Dunning *et al.* 2018).

Climate change models also predict changes in the patterns of precipitation in terms of the total amount and intensity of rainfall events (IPCC 2013) and this will affect grassland plant composition and biomass (Barnett & Facey 2016). Changes in precipitation can have indirect effects on plants as different plants respond differently in different amounts of rainfall, the impact of herbivory on plant diversity also varies across precipitation gradients (Olf and Ritchie 1998). With reduced grass biomass production and quality as a result of reduced rainfall herbivores that rely on this grass also suffer (Wu *et al.* 2011).

1.3.2. Temperature

Climate change is the most challenging global problem that is evident with rapid global warming (Chen *et al.* 2015). It has been reported that the global mean atmospheric temperatures increased by 0.85 °C between 1880 and 2100 (IPCC 2013). It is expected that increased temperatures will lead to increased evapotranspiration as a result of climate change and drier soils leading to more soil moisture losses and ground water recharge (Shahid *et al.* 2017). According to IPCC, the atmospheric temperature was expected to increase between 1 °C and 3.5 °C as a result of increased GHG by the end of the 20th century (Houghton 1996).

It is expected that this global warming pattern will increase through the twenty-first century under all representative concentration pathways (Hassan & Hashim 2020). Intensified

levels of manufacturing are also likely to increase GHG emissions (Abbasnia & Toros 2016). The episodes of El Niño-Southern Oscillation (ENSO) events in Africa are linked to climate change (Korcha & Sorteberg 2013). African biodiversity is also expected to be lost as a result of increased climate change during the twenty-first century (Sala *et al.* 2000). It is important to understand the relationship between ecosystem services climate change and biodiversity as they are all related (Sintayehu 2018). Studies documented that in future the wet seasons will get wetter, whereas dry seasons will get drier (Chou *et al.* 2013).

1.4. Direct and indirect effects of climate change on rangeland production

1.4.1. Effect on rainfall on rangeland production

Overgrazing is the result of poor rangeland management that leads to degradation. This can result in poor regeneration of plants, biodiversity reduction and poor livestock productivity (Tietjen *et al.* 2010). Global warming and climate change will surely increase this risk. Arid and semi-arid rangelands are threatened by decreasing mean annual rainfall as a result of climate change (Dore 2005). The number of extreme events increases, whereas the frequency of rainfall events decreases (Easterling *et al.* 2000). It is likely that with higher temperatures, evapotranspiration will intensify water stress for plants (Hughes 2003). These changes do not affect plant types equally as some plants are more susceptible to water stress than others. Grass cover was found to decrease at mean annual rainfall below 650 mm in semi-arid and arid savannas, whereas the woody cover increased linearly (Sankaran *et al.* 2005).

Soil moisture in the subsoil is also affected by rainfall events as it is recharged when they are intense or clustered (Tietjen *et al.* 2010). Soil moisture fluctuations in the topsoil layer are more rapid than in the subsoil as more evaporation occurs in this layer than the subsoil layer (Schwinning & Ehleringer 2001). Plant root access to soil moisture in the subsoil depends on the plant potential rooting depth and differs from species to species (Fravolini *et al.* 2005). In countries such as the United States, effects of climate change are already evident on water resources because of alterations in rainfall patterns, type, intensity and occurrence of drought (Karl and Melillo 2009). Stress is added to nations to manage water resources properly as a result of altering rainfall, runoff patterns and temperature (Baron *et al.* 2013).

Rainfall reduction as a result of climate change may also lead to desertification because of regional availability of water, vegetation cover variation and soil moisture (Wand *et al.*

1999). According to several global climate models, desertification in Africa is linked to drought, which is associated with the warming of the Indian and Pacific oceans (Giannini *et al.* 2008). According to climate models, soil moisture over larger areas of the semi-arid grasslands in Asia and North America may be reduced by global warming (Seneviratne *et al.* 2010). The key variable controlling numerous processes on the land is the water stored in the soil. A source of water for the atmosphere is the soil moisture through the processes that lead to evapotranspiration from the land and these include bare soil evaporation and transpiration (Oki & Kanae 2006). More than half of the total solar energy absorbed by land surfaces is used by land evapotranspiration (Trenberth *et al.* 2009). Reduced rainfall may result in reduced grass production which will negatively affect livestock production.

1.4.2. Historical changes and patterns

The fourth climate change assessment report revealed that there is evidence that the climate is changing and that global warming is undisputable (Le Treut *et al.* 2007). These changes include global mean temperatures, global average sea level, and the extent of Arctic sea ice (Stott *et al.* 2010). Although there is no doubt that the earth is warming, there is no certainty about what causes these changes. However, drivers of climate change such as human-induced emissions of GHG and volcanic eruptions could be causing sustained climate changes.

The current increase in global temperatures did not occur by chance in a stationary climate (Zorita *et al.* 2008). This increase in temperature and in geographical patterns were detected by studies (Barnett *et al.* 2005). These patterns are normally based on climate simulations and observations of sophisticated statistical analysis. Climate change has also affected the distribution and interactions of biological communities (Butler 2019). These changes have been associated with invasive species (Stephens *et al.* 2019) and reduced habitat for some species (Sekercioglu *et al.* 2008). In the Western Cape in South Africa, climate change resulted in fire and invasive species, leading to a decline in plant biodiversity in the Fynbos biome (Slingsby *et al.* 2017). A decrease of between 1.9% and 2.7% in annual rainfall per decade was observed between 1975 and 2010 (Ziv *et al.* 2013).

1.4.3. Forecast scenarios

Drier conditions because of climate change have been observed in the eastern Mediterranean region in recent decades (Ziv *et al.* 2013). In addition, a further decrease of up

to 20% in annual rainfall can be expected by 2050 (Evans 2009). Ecosystem services and functions could be seriously affected by rainfall regime changes since plant growth is affected directly by water availability (Sternberg *et al.* 2015). When predicting primary production as a result of future climate impacts both total annual rainfall and its inter-annual variability need to be taken into consideration since both parameters affect the primary production (Golodets *et al.* 2015). A study predicted that temporal and spatial variability in rainfall had a higher potential effect on primary production than average conditions in semi-arid and arid regions (Tietjen & Jeltsch 2007). The increase in summer temperatures combined with a decrease in mean annual rainfall (Shohami *et al.* 2011) will have an impact on shrub survival, which promotes the growth of annual plants (DeMalach *et al.* 2014), which indirectly affects herbaceous primary production on top of the direct effects of reduced rainfall on herbaceous primary production.

Where an important ecosystem service is forage production (Golodets *et al.* 2015), future changes in rainfall regime will result in high vegetation vulnerability in the semi-arid and arid ecosystems (Tietjen & Jeltsch 2007). The simulation models of climate change predict an increase in vegetation patches (Shafran-Nathan *et al.* 2013). Global ecosystems are affected by climate change as the habitat structure and the environmental conditions influence species composition, phenology and range shifts (Chen *et al.* 2011). Furthermore, environmental degradation, which is human made and causes habitat loss and fragmentation (Sternberg *et al.* 2015). Ziv *et al.* (2013) predicted an increase in frequency of extreme weather events, including rise in sea-level, sea water temperature, periods of intense heat, floods and drought. Some native species will disappear because of environmental conditions that favour invasive species because of climate change (Sternberg *et al.* 2015). Ecosystem services and functions such as ANPP are expected to be affected by changes in rainfall as plant growth depends on water availability (Köchy *et al.* 2008).

1.4.4. Effect on soil conditions

Soil is the growing medium for all vegetation and all animals rely on plants for their survival. One of the global challenges to plant productivity is water availability (Lambers *et al.* 1998). Water is not the only limiting factor in drought-stricken regions, but also nutrients such as nitrogen (Harpole *et al.* 2007). South African soils are also vulnerable to these increases in temperatures owing to climate change (Ziervogel *et al.* 2014). A significant threat is posed by

climate change to South African water resources, health, food security, infrastructure and ecosystem services and its biodiversity (Ziervogel *et al.* 2014). There is growing evidence that plant rarity, invasion, community attributes and plant species coexistence are influenced by plant-soil feedbacks (Van der Putten *et al.* 2013). Some studies have shown that drought may have long-lasting effects on ecosystem services and plant growth (Kaisermann *et al.* 2017).

Because the total cropped area depends on uncertainties of the rainy seasons, this indicates that agriculture is climate dependent. Agriculture is regarded as both the victim of and the contributor to climate change (Pareek 2017). It is considered a contributor because of the significant amounts of the GHG that are emitted by animals and machines that are used in this industry and a victim because of the negative impacts of climate change on agricultural production. Plants have to absorb nutrients from the soil through soil solution pool. However, without water this is impossible. There is no certainty about how the changes in evaporative demand versus rainfall will force the forecast drought changes (Trenberth *et al.* 2014).

Soil water content (SWC) is another important component in plant production as it has a direct influence on plant yield and growth. Climate change is also expected to lead to a decrease in SWC, which will lead to increased effects on the agricultural sector. The agricultural water resources will be affected by SWC, especially in arid and semi-arid regions (Liu and Shao 2014).

1.5. Effect of resting period on rangeland productivity

The overall productivity of vegetation could be affected significantly by grazing (Christensen *et al.* 2003). According to Numata *et al.* (2007), there is a relationship between cattle stocking rate and a spectral vegetation index, which can be used for long-term monitoring. The effect of grazing pressure on arid and semi-arid rangelands has been used as a tool to study the response of the ecosystem to grazing to inform sustainable rangeland management (Wesuls *et al.* 2013). Therefore, it is important to know how vegetation and different species will respond to grazing to make informed sustainable rangeland management decisions. Until now rangeland ecologists have made a clear distinction between increasers and decreasers with regard to indicator species for grazing impact (Vesk & Westoby 2001).

Increase grass species have a greater range of response in the southern African grass species (Trollope 1990). Grasslands are prone to disturbances, which are strongly caused by fire and grazing regimes (Milchunas *et al.* 1988). Ecosystem functioning, diversity patterns on multiple scales and grassland species composition are affected by disturbance such as grazing (Knapp *et al.* 1998). It has been reported that climate change (Chapin 1993) or ecosystem functioning under disturbance could best be described by reduced sets of traits such as life forms (Chapin 1993).

1.6. Conclusion

Reduced rainfall is likely to negatively affect rangeland productivity and production. This poses an increasing challenge to rangelands and users. Finding ways to mitigate these challenges is of paramount importance. There is also a need to reduce the economic and ecological impacts of reduced rainfall. Rangeland users also need to know the importance and the duration of resting periods. This will require ecological research that will look at the impacts of reduced rainfall and resting period on rangeland productivity in terms of above biomass and soil properties. It is also necessary to understand how rangeland will respond to rainfall interception and resting periods. The research must look at how the rainfall interception will affect ecological groups (grasses and forbs). Such information can be used on climate models to predict the future effects of climate change on grassland productivity and warn against the future occurrence of drought. This will be useful in planning for future droughts in the long term.

Better planning and mitigation strategies may come with the research based on this rainfall interception and resting period. Information provided by the results of this study will make it clearer and easier for the rangeland managers to mitigate the impacts of future droughts on rangeland productivity. The study demonstrates the interaction between social/economic and ecological systems that would take place as changes in rainfall variability occur as the farmers will have to buy more feed for their animals with the decrease in the aboveground biomass.

Managers who know how these interactions work are likely to make better informed decisions that involve the types and numbers of animals that can be kept on a particular camp. These will include destocking on overstocked rangelands to avoid overgrazing. There is little

information about the effects of rainfall interception and resting period in South Africa. Therefore this study was conducted to determine the effect of rainfall interception and resting period on grassland productivity to determine how these grasslands would look in future as a result of predicted future droughts and grazing livestock. There is a need to monitor long-term effects of grazing on ecosystem processes and biological dynamics as they are poorly studied in the semi-arid ecosystems of South Africa.

1.7. Specific objectives

The research was conducted with these objectives:

- To assess the effect of rainfall interception and resting period on residual soil water content and selected soil chemical properties of the semi-arid grassland. It is expected that interception in rainfall and grazing could affect (negatively or positively) the residual soil water content and other soil elements that are important for plant growth.
- To evaluate annual net primary productivity of various functional groups as affected by different intensities of rainfall interception in the semi-arid grasslands of Gauteng in South Africa. It is expected that rainfall interception will have a negative effect on the annual net primary productivity. However, the extent to which it will affect the country's rangelands is not known.
- To investigate seasonal herbaceous structure and biomass production response to rainfall interception and resting period in the semi-arid grassland area of South Africa. It is expected that the seasons will have different effects on herbaceous layer.
- To determine effect of rainfall interception and resting period on soil seed bank of grassland in Gauteng, South Africa. It is expected that rainfall interception and resting period will affect the soil seed bank because of removal of seeds through cutting and the lack of seeds because of non-productivity of plant as a result of water shortage.

Chapter 2

Effect of rainfall interception and resting period on residual soil water content and selected soil chemical properties

2.1 Abstract

Water deficit associated with rainfall reduction is a recurring event, which is forecast to increase in intensity and frequency over the next decades as a result of climate change. Changes in rainfall regimes have intensified the hydrological cycle as a result of climate change in South Africa. However, the influence of changes in rainfall regimes on residual soil moisture, biological and physicochemical properties of soil are spatially and temporally variable, depending on their duration and extent, other climatic factors, soil condition, vegetation cover and grazing management implemented in the area. The objective of this study was to investigate the effect of rainfall interception and resting period on residual soil water content and selected soil chemical properties of the semi-arid grassland. A split plot experimental design was used to investigate the interactive effect of rainfall interception (0%, 15%, 30% & 60%), resting period (70 and 90 days) on soil properties in semi-arid grasslands of South Africa at a depth of 20 cm. Rainfall interception of 60% affected residual soil water content negatively, this may influence regrowth potential after defoliation by grazing or cutting of natural grasslands.

Key words: climate change, rainfall, soil pH, total nitrogen

2.2. Introduction

Water deficit owing to reduced rainfall is a recurring event, which is forecast to increase in intensity and frequency over the next few decades as a result of climate change (IPCC 2013). A shortage of water has been identified as one of the biggest threats to agricultural production around the globe (Lesk *et al.* 2016). This could affect grasslands negatively, which are the main source of feed for livestock (Meisser *et al.* 2019). Degradation caused by climate change, including desertification and soil erosion, is one of the problems that threaten the socioeconomic development. (Sun *et al.* 2015; Guo *et al.* 2019). In response to climate change, rainfall regimes have been altered and the movement of water above and below soil surface has intensified (Park *et al.* 2016). Alterations in rainfall affect plant net primary productivity significantly (Knapp *et al.* 2017). These changes have indirect and direct effects on the biological and physicochemical properties of soil (Landesman & Dighton 2010). Because of this, it is imperative to understand how current and future water deficits will affect the soil moisture and physical and chemical properties.

Changing rainfall regimes may alter the response patterns of soil properties (soil quality) differently in different vegetation types (Ren *et al.* 2018). Doran and Parkin (1994) defined soil quality as the capacity of a specific kind of soil to function, within natural or managed ecosystem boundaries, to sustain plant and animal productivity, to maintain or enhance water and air quality, and to support human health and rehabilitation. Climate change expressed in the form of rainfall reduction may reduce soil nutrient uptake by plants owing to reduced soil water content (SWC) altering the metabolic state of the plant through reduced plant growth and thereby its capacity to absorb nutrients (Sardans *et al.* 2008a). Several studies showed that low rainfall reduced plant growth and nutrient uptake by lowering soil moisture and respiration rates (Grabarova & Martinkova 2001; Wang *et al.* 2005; Protoćić *et al.* 2005; Singh & Singh 2006; Hu *et al.* 2007; Sardans *et al.* 2008a).

Besides its key functions in photosynthesis and transpiration, soil moisture is the medium through which plants acquire nutrients from the soil (Fischer *et al.* 2019). A growing body of research has sought to understand the ecological response of rangelands through imposing experimental droughts (Grime *et al.* 2008; Reichmann *et al.* 2013). These have been the leading methods of studying the impact of drought and of the ways in which water deficits have affected ecosystem processes for the past two decades (Hoover *et al.* 2018). Although

drought experiments abound in the literature, and the method is simple, the responses of ecological variables have been highly inconsistent. Hence patterns and mechanisms of drought sensitivities across the ecosystems have not been easy to determine (Smith *et al.* 2017).

The diverse processes of the nitrogen (N) cycle can be altered by water deficit in the soil. However, the effects are site specific, reflecting the complexity of the process (Meisser *et al.* 2019). Bioavailability of phosphorus (P) is affected by factors such as soil moisture, sources of P, and soil pH (Dijkstra *et al.* 2015; Shen *et al.* 2011). Drought may also alter P cycling through lower diffusion rates (Lambers *et al.* 2008) and lower desorption (Belnap 2011). Rainfall interception can reduce availability of potassium (K), Ca (Sardans *et al.* 2008a) and P through reducing mineralization rates (Sardans & Peñuelas 2005). On the other hand, P and K are removed through absorption by the plants from the soil (Sardans & Peñuelas 2007). Nonetheless, there are few studies, if any, on the impact of various levels of drought on the availability of soil nutrients essential to plant growth such as P, K, calcium (Ca), sodium (Na), chlorine (Cl), magnesium (Mg), sulphate (SO₄) and nitrate (NO₃). Establishing the effect of various levels of rainfall interception on the availability of essential nutrients and the residual rainfall for the next season is crucial to establish adaptation and mitigation measures associated with climate change. The aim of this study was to determine the interactive effect of simulated climate change expressed through rainfall interception and resting period on soil residual water content and selected soil physical and chemical properties in the semi-arid grassland area, South Africa.

2.3 Materials and methods

2.3.1. Site description

The study was conducted at Hatfield Experimental Farm, University of Pretoria. The farm is situated at an altitude of 1372 m above sea level. The coordinates of the study sites are 28° 16' E and 25° 45' S. The farm is situated in a summer rainfall area with long-term mean annual rainfall of 674 mm. The soil on the farm is categorized as non-calcareous with a homogenous red colour and weak structure of Hutton form and is sandy loam with 20–35% clay (Soil Classification Working Group 1991) with a pH of 6 in a 2.5 to 1 soil-water ratio. The study site has not been grazed for more than 60 years. The rainfall interception research was conducted with rainout shelters (Magandana *et al.* 2021) constructed on natural semi-arid

grassland vegetation (Mucina & Rutherford 2006) on a homogenous range condition. The soil texture at various levels of rainfall interception is shown on Table 2.1.

Table 2.1 Soil textural analyses of rainfall interception treatments, University of Pretoria Experimental Farm, Pretoria

Rainfall interception	Sand %	Clay %	Silt %
0%	53.1	32.1	14.9
15%	50.7	35.6	16.9
30%	48.7	33.8	17.5
60%	51.2	34.3	14.4
Standard deviation	1.8	1.5	1.5

2.4.2. Rainout shelters and resting periods

Rainout shelters were established as described by Yahdjian & Sala (2002) as shown in figure 2.1.. Rainfall interception was employed as main plot treatment at four levels, namely 0%, 15%, 30%, and 60%. Each treatment was replicated five times and within each treatment, as main plot, two resting periods (70 and 90 days) over seasons (spring, summer and autumn) were adopted as sub-plot (7m x 3.5m) treatments in a split plot experimental design modified from Talore (2015). The main plots were 49 m² (7 m x 7 m) in size and were covered with metal frame structures with V-shaped clear acrylic bands on top without ultraviolet. The bands were constructed with a longitudinal plate of 120° angle. A mean height of 1 m was maintained at the lowest side of the shelter. Water was collected from the acrylic material and channelled away from the plots through gutters. Ambient rainfall was measured after each rainfall event using five rain gauges that were scattered over the experimental site. A 25 cm ditch was excavated along the boundary of the experimental site to avoid water runoff into the plots.



Figure 2.1. Rainout shelter.

2.4.3. Soil sampling analysis

In August 2018, two soil samples per sub-plot (70- and 90-day resting period) were collected using a 1005 cm³ volume (8 cm inner diameter, 20 cm length) core sampler. The two sub-samples per sub-plot were bulked to make a homogeneous soil sample. The samples were placed in clearly marked plastic bags and transported to the laboratory for analysis. The soil samples were oven dried at 40 °C for 48 hours before being sieved through a 2-mm sieve to remove stones and roots. The samples were kept in the laboratory pending analysis.

Soil textural class analyses were conducted on samples using the Bouyoucos hydrometer method (Bouyoucos 1962). Textural classes were classified using the textural triangle (Thien 1979). Soil pH (H₂O) was determined with a digital pH meter (Fisher Scientific™ Accumate™ AB15+, Basic and Biobasic™ pH/mV/oC meters) in 1 to 2.5 soil to water suspension. Total P in the soil samples was determined after wet acid digestion using an inductively coupled plasma optical emission spectrometer (ICP-OES) (SpectroFlame Modula, Spectro, Kleve, Germany). The wet acid digestion was conducted on a ground 0.5 g sample, which was digested with 7 mL of HNO₃ (concentrated nitric acid, 650 mL.L⁻¹) and 3 mL of HClO₄ (perchloric acid, 700 mL.L⁻¹) at temperatures up to 180 °C. This was followed by the gradual addition of 0.5 mL of H₂O₂ (hydrogen peroxide, 500 mL. L⁻¹) and further heating for 20 minutes.

The digestate was removed from the block to partially cool down for about 10 min. Finally, 10 mL of a 1:1 (v/v) hydrochloric acid solution was added and shaken to mix before transfer to a 100 mL volumetric flask. Soil samples were ground to pass through a 150 μ m screen and analysed for percentage C and total N using a Carlo Erba NA1500 C/N analyser (Carlo Erba Strumentazione, Milan, Italy). Soil samples were extracted in 1:5 (v/v) 1 mol. L⁻¹ KCl and tested for ammonium and nitrate with a Lachat autoanalyser (Lachat Quick Chem Systems, Milwaukee, WI, USA). Soil electrical conductivity was analysed in 1:2 (v/v) soil/water ratio extracts using a Beckman conductivity bridge and reported in units of mS m⁻¹.

2.4.4. Soil water content measurement

Soil water content measurements were conducted towards the end of each season (summer and autumn) just before the herbage was cut. A neutron water meter (Model 503 DR CPN hydroprobe; Campbell Pacific Nuclear, Ca) was used to measure soil water content (SWC) at three soil depths (0–20 cm, 20–40 cm and 40–60 cm) immediately before harvesting the vegetation at various rainfall interceptions and resting periods. Profile SWC was determined as the sum of the three soil layers.

2.4.5. Data analysis

Soil chemical and physical data were subjected to general linear model analysis of variance (ANOVA) procedure (Proc GLM) of SAS (2008). The rainfall interceptions and resting periods were regarded as the fixed effects. The model was designed to determine whether rainfall interception and resting period had significant effect on soil nutrient composition and residual soil water content. The plots were split into two, with one side herbaceous layer cut after 70 days while the other side was cut after 90 days. Soil samples were taken at both cutting intervals. Where treatment effects were significant ($P < 0.05$), the means were separated using Tukey's test.

The model is:

$$Y_{ijkl} = \mu + \alpha_i + df_{j(i)} + g_k + \alpha g_{ik} + df g_{j(i)k} + \alpha df g_{ijk} + e_{ijkl}$$

Where y is an observation variable (soil chemical and physical properties) and SWC

μ , overall mean

α_i , effect of rainfall interception, RI ($i = 0\%, 15\%, 30\%$ and 60%)

$df_{j(i)}$, effect of resting period within RI [$j(i) = 70$ and 90 days (RP)]

g_k , effect of the season ($k = 1, 2$)

h_{ik} , effect of depth ($ik = 0-20$ cm, $20 - 30$ cm, $30 - 40$ cm)

$\alpha_{df\ i(j)}$, interaction between RI and RP

$df_{j(i)k}$, interaction between season and RP

$\alpha_{dfg_{ijk}}$, interaction between RI, RP, depth and season

e_{ijkl} , a random or unexpected error

2.5 Results

2.5.1 Effects of rainfall interception, resting period, and soil depth on residual soil water content

Residual soil moisture content readings collected towards the end of the rainy season did not show any significant ($P > 0.05$) interaction effect between rainfall reduction, resting period and soil depth for all possible combinations (Table 2.2). Residual soil water content, however, was affected significantly by the main effects of rainfall reduction, resting period, and soil depth. Generally, residual soil water content was relatively higher in autumn than summer for 15% rainfall interception (Figure 2.2), whereas the difference between seasons was not significant for 0%, 30% and 60% rainfall reduction. During summer, 30% rainfall interception treatment had a significantly ($P < 0.05$) higher residual soil water content than the 15% and 60% treatments (Figure 2.2). Residual soil water content in autumn was highest for the 0% interception and lowest for the 60% interception, whereas the 15% and 30% interception levels remained the same.

Table 2.2. Residual soil moisture as affected by rainfall interception, resting period, soil depth and their interactions

Effects	RI	RP	Depth	RI*RP	RI*Depth	RP*Depth	RI*RP*Depth
DF	3	1	2	3	6	2	6
P-value	0.04*	<0.01**	<0.001***	0.58NS	0.45NS	0.24NS	0.51NS

NS: non-significant at $P > 0.05$; * $P < 0.05$; ** $P < 0.01$, *** $P < 0.001$

DF: degree of freedom, RI: rainfall interception, RP: resting period

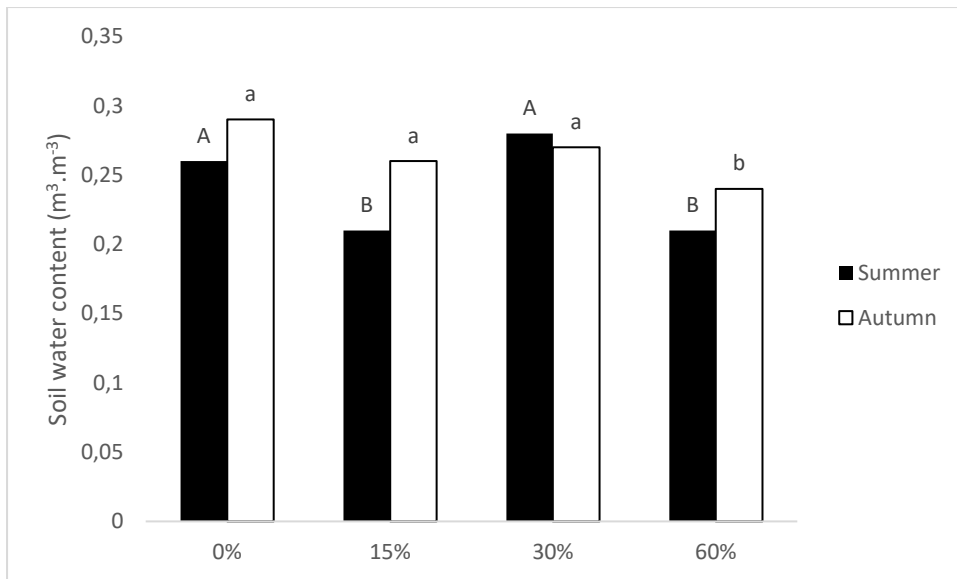


Figure 2.2 Mean ($\pm$ SE) response of residual soil water content to rainfall interception over summer and autumn

There was a significant ($P < 0.05$) increase in SWC with depth for both summer and autumn (Figure 2.3). Between seasons, residual soil water content was generally higher in autumn than in summer at 0–20 cm soil depths (Figure 2.3). It was also apparent that the shorter resting period of 70 days increased ($P < 0.05$) residual soil water content than the longer resting period of 90 days in the summer and autumn (Figure 2.4).

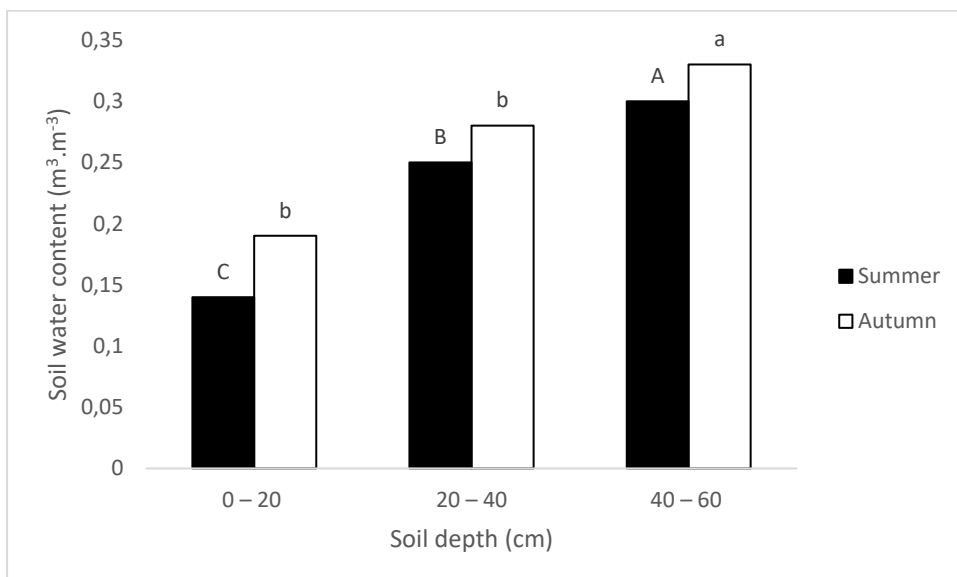


Figure 2.3 Mean ($\pm$ SE) response of residual soil water content to soil depth in summer and autumn

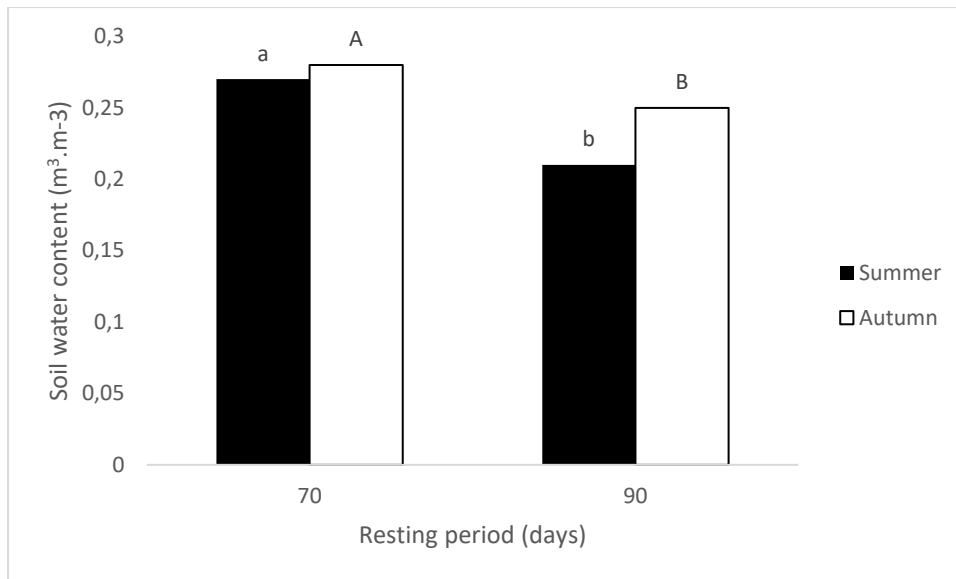


Figure 2.4 Mean ($\pm$ SE) response of soil water content to resting period in summer and autumn

2.5.2. Effects of rainfall interception and resting period on soil pH, salinity, carbon, nitrate and macro nutrients

There was a significant ($P < 0.05$) interaction effect between rainfall interception and resting period on soil pH (Table 2.3, Figure 2.5). There was no significant ($P > 0.05$) rainfall interception and resting period interaction effect on soil electrical conductivity, nitrogen and percentage carbon (Table 2.4). Similarly, resting period did not affect soil electrical conductivity ($P > 0.05$). Soil electrical conductivity, however, was ($P < 0.01$) affected by rainfall interception (Table 2.4). Hence, lowest electrical conductivity ($49.5 \pm 7.88 \text{ mS cm}^{-1}$) was recorded in the 0% rainfall interception and highest ($93.2 \pm 7.88 \text{ mS cm}^{-1}$) under the 60% rainfall interception. Similarly, total soil nitrogen and carbon content did not show ($P > 0.05$) difference among rainfall interception levels and between resting periods. There was a ($P < 0.05$) rainfall interception and resting period interaction effect for soil NO_3 , P and K content (Figure 2.5). Soil nitrate was significantly higher at 60% rainfall interception and 90-day resting period compared with the rest of the treatments.

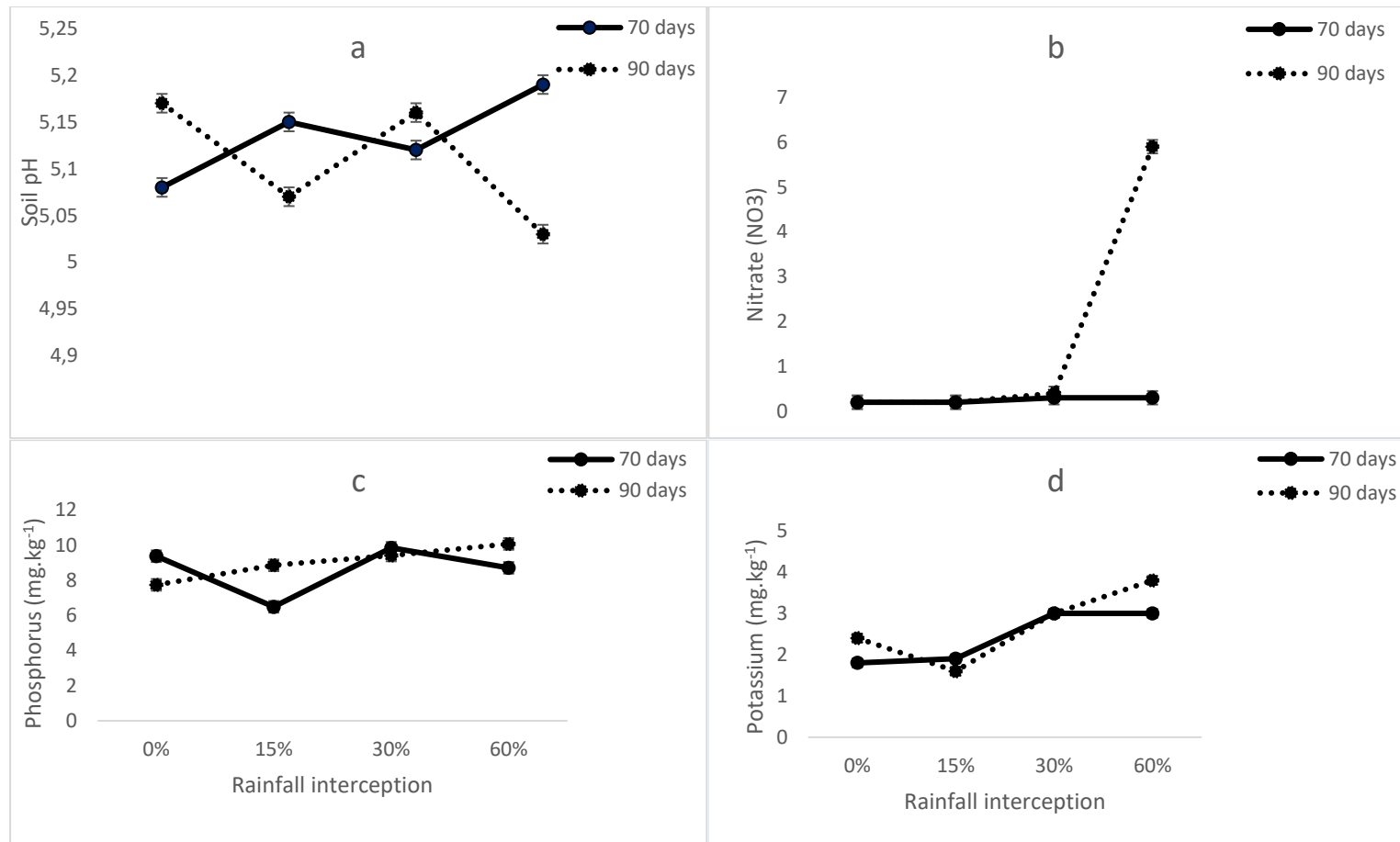


Figure 2.5. Interaction between resting period and rainfall interception on soil a) pH, b) nitrate (NO₃) (mg.kg⁻¹), c) phosphorus (mg.kg⁻¹) and d) potassium (mg.kg⁻¹)

Table 2.3. Partial ANOVA table showing the degrees of freedom and *P*-values from restricted estimation of maximum likelihood analysis at ($\alpha=0.05$) for soil (mean $\pm$ standard error) pH, electrical conductivity (mS/cm), total nitrogen (mg.kg⁻¹), carbon (%), nitrate (mg.kg⁻¹), phosphorus (mg.kg⁻¹) and potassium (mg.kg⁻¹) at various rainfall interceptions, resting periods and their interactions

Effects	DF	pH	EC (mS/cm)	Nitrogen	%Carbon	Nitrate	Phosphorus	Potassium
RI	3	0.58NS	<0.01**	0.63NS	0.35NS	<0.0001	<0.01**	<0.0001**
0%		5.13 $\pm$ 0.01	49.5 $\pm$ 7.88 ^b	1.0 $\pm$ 0.07	1.64 $\pm$ 0.03	0.04 $\pm$ 1.24 ^b	8.55 $\pm$ 0.33 ^{bc}	2.10 $\pm$ 0.08 ^c
15%		5.11 $\pm$ 0.01	51.3 $\pm$ 7.88 ^b	0.9 $\pm$ 0.07	1.65 $\pm$ 0.03	0.04 $\pm$ 1.24 ^b	7.67 $\pm$ 0.33 ^c	1.78 $\pm$ 0.08 ^d
30%		5.14 $\pm$ 0.01	76.1 $\pm$ 7.88 ^a	1.1 $\pm$ 0.07	1.72 $\pm$ 0.03	0.13 $\pm$ 1.24 ^b	9.63 $\pm$ 0.33 ^a	2.99 $\pm$ 0.08 ^b
60%		5.11 $\pm$ 0.01	93.2 $\pm$ 7.88 ^a	0.9 $\pm$ 0.07	1.58 $\pm$ 0.03	17.58 $\pm$ 1.24 ^a	9.39 $\pm$ 0.33 ^{ab}	3.40 $\pm$ 0.08 ^a
RP	1	0.12NS	0.10NS	0.17NS	0.06NS	<0.0001	0.22NS	<0.001**
70 days		5.14 $\pm$ 0.01	60.7 $\pm$ 0.10	0.9 $\pm$ 0.05	1.66 $\pm$ 0.02	0.08 $\pm$ 0.88 ^b	8.60 $\pm$ 0.23	2.42 $\pm$ 0.05 ^b
90 days		5.11 $\pm$ 0.01	74.3 $\pm$ 0.10	1.0 $\pm$ 0.05	1.63 $\pm$ 0.02	8.82 $\pm$ 0.88 ^a	9.02 $\pm$ 0.23	2.71 $\pm$ 0.05 ^a
RI*RP	3	<0.001***	0.27NS	0.51NS	0.31	<0.0001	<0.01**	<0.001**

NS: non-significant at $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

DF: degree of freedom, RI: rainfall interception, RP: resting period, EC: electrical conductivity

2.5.3. Effects of rainfall interception and resting period on selected nutrients (calcium, magnesium, sodium, chlorine, sulphate, anions and cations)

There was a highly ($P < 0.05$) rainfall interception and resting period interaction effect on soil Ca, Mg, Na, Cl, SO_4 , anion and cation content (Table 2.4). Similarly, rainfall interception and resting period highly ($P < 0.05$) affected soil Ca concentration. Soil Ca content was highest for the 60% rainfall interception and lowest for the 15% (Table 2.4). In terms of resting period, soil Ca content was highest under the 90-day resting period compared with the 70-day rainfall interception (Table 2.4).

There was a highly ($P < 0.0001$) rainfall interception and resting period interaction effect on soil Mg content (Figure 2.6). Soil Mg content was also highly ($P < 0.0001$) affected by rainfall interception and resting period independently (Table 2.4). Similar to Ca, soil Mg content was highest for 60% rainfall interception and lowest for 15% (Figure 2.6 b). Soil Mg content was higher under the 90-day resting period than the 70-day resting period (Table 2.4). Unlike the soil Ca and Mg contents, rainfall interception and resting period had no ($P < 0.05$) effect on soil sodium (Na) content, despite a ($P < 0.05$) rainfall interception and resting period interaction effect (Table 2.4) on soil Na.

There was a statistically ($P < 0.01$) rainfall interception and resting period interaction effect on soil chlorine (Cl) content (Table 2.4). Generally, soil Cl concentration was similar among treatments except for the 15% rainfall interception level, which was statistically highly ($P < 0.05$) lower than the rest of the treatments (Figure 2.6 d). There was a statistically highly ($P < 0.0001$) rainfall interception and resting period interaction effect on soil SO_4 concentration (Table 2.4). Both rainfall interception and resting period independently affected the concentration of SO_4 in the soil ($P < 0.05$). Resting the veld for 90 days resulted in higher soil SO_4 concentration than 70 days of resting period, whereas soil SO_4 concentration was highest for the 60% rainfall interception and lowest for the 0% rainfall interception (Table 2.4).

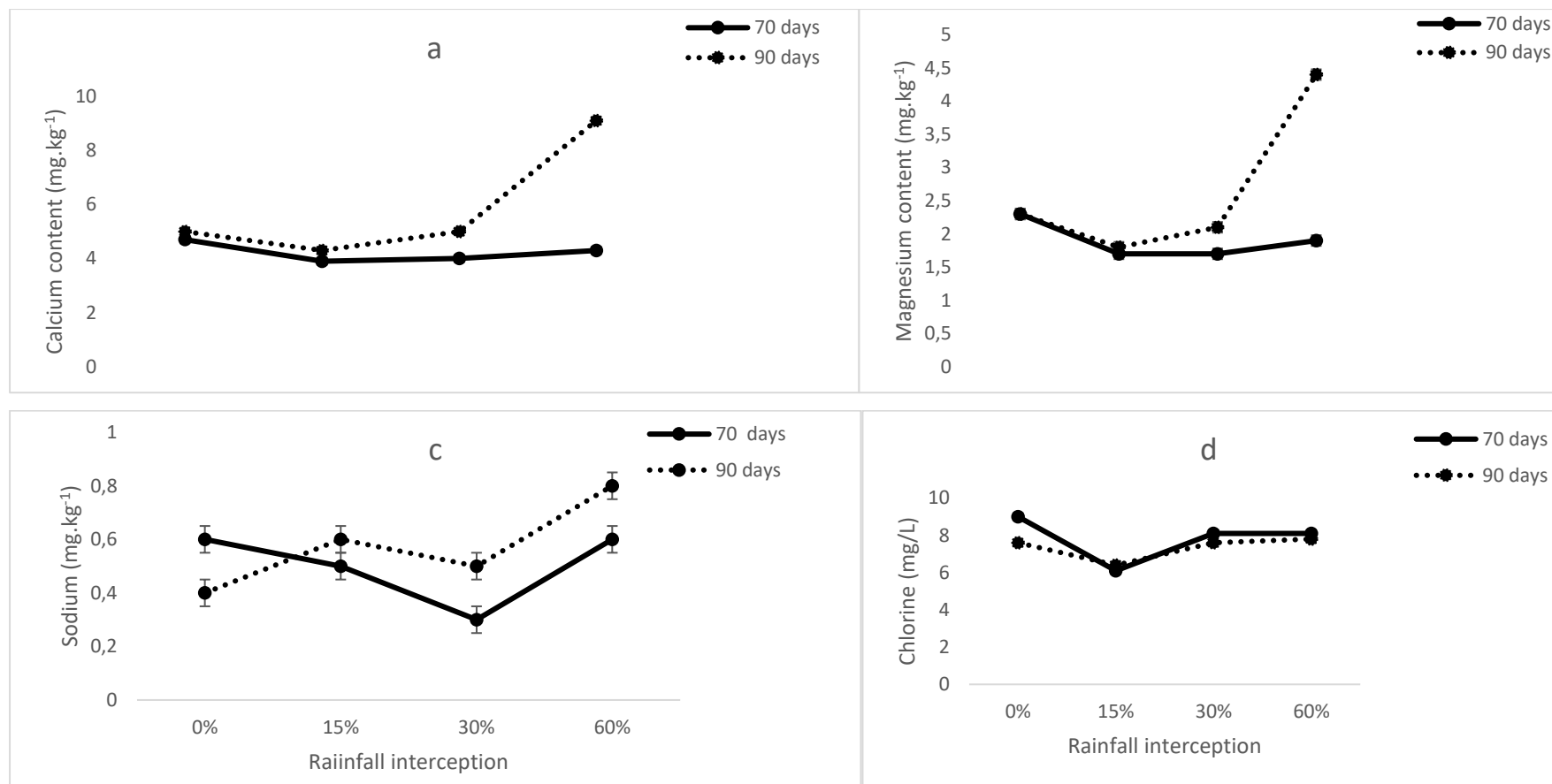


Figure 2.6 Interaction between resting period and rainfall interception on soil a) calcium (mg.kg⁻¹), b) magnesium (mg.kg⁻¹), (c) sodium (mg.kg⁻¹) and (d) chlorine (mg/L)

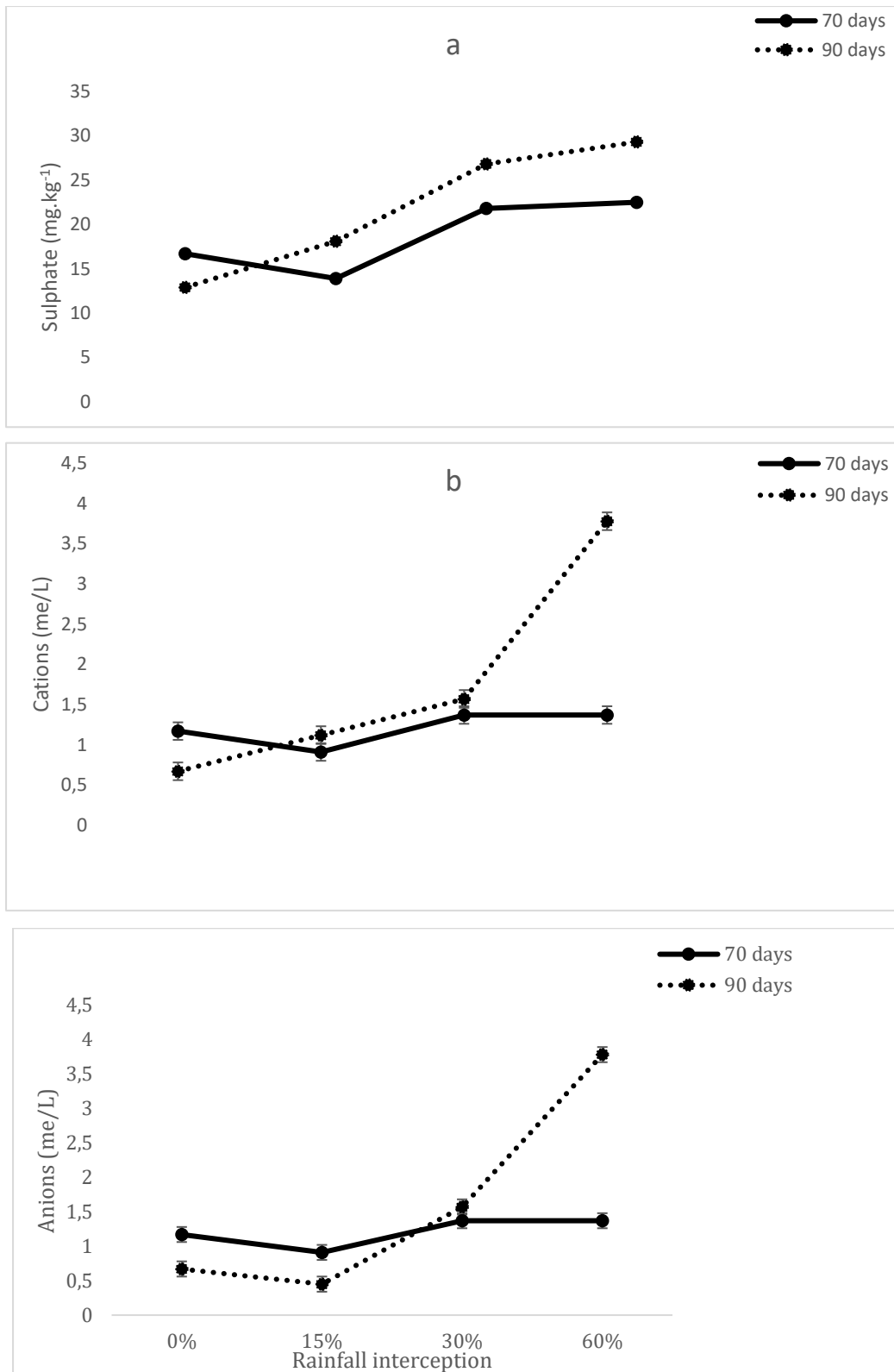


Figure 2.7 Interaction between resting period and rainfall interception on soil a) sulphate (mg.kg⁻¹), b) anions (me/L) and c) cations

Table 2.4 Effects of rainfall interception and resting period on selected micro nutrients anions (me/l) and cations (me/l)

Effects	DF	Ca	Mg	Na	Cl	SO ₄	Anions	Cations
RI	3	<0.0001***	<0.0001***	0.1099NS	<0.0001***	<0.0001***	<0.0001***	<0.0001***
0%		4.8±0.10 ^b	2.3±0.05 ^b	0.5±0.09	8.3±0.14 ^a	14.8±0.10 ^d	0.9±0.11 ^c	0.9±0.11 ^c
15%		4.1±0.10 ^d	1.7±0.05 ^d	0.5±0.09	6.3±0.14 ^b	16.0±0.10 ^c	0.7±0.11 ^c	0.7±0.11 ^c
30%		4.5±0.10 ^c	1.9±0.05 ^c	0.4±0.09	7.9±0.14 ^a	24.3±0.10 ^b	1.5±0.11 ^b	1.5±0.11 ^b
60%		6.7±0.10 ^a	3.0±0.05 ^a	0.7±0.09	7.9±0.14 ^a	25.9±0.10 ^a	2.6±0.11 ^a	2.6±0.11 ^a
RP	1	<0.0001***	<0.0001***	0.4577NS	0.0035**	<0.0001***	<0.0015**	<0.0001***
70 days		4.2±0.07 ^b	1.9±0.04 ^b	0.5±0.06	7.8±0.10 ^a	18.7±0.07 ^b	1.2±0.08 ^b	1.2±0.05 ^b
90 days		5.8±0.07 ^a	2.6±0.04 ^a	0.6±0.06	7.4±0.10 ^b	21.8±0.07 ^a	1.6±0.08 ^a	1.8±0.05 ^a
RI*RP	3	<0.0001***	<0.0001***	0.0365*	0.0077**	<0.0001***	<0.0001***	0.0001***

NS: non-significant at $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

DF: degree of freedom, RI: rainfall interception, RP: resting period, Ca: calcium, Mg: magnesium, Na: sodium, Cl: chlorine, SO₄: sulphate

2.4. Discussion

This study investigated the interactive effect of simulated climate change expressed through rainfall interception and grazing resting on residual extractable cations, anions, electric conductivity, soil C, and residual soil water content. Residual soil water content plays a significant role in the revegetation of natural rain fed grasslands after harvest and intensive grazing (Guo *et al.* 2020). Residual soil water content was higher in autumn than summer, which agreed with the findings of Fan *et al.* (2018). Fan *et al.* (2018) also reported higher residual soil moisture in spring and autumn than summer and winter. This was attributable to the higher water usage and transpiration by plants during summer, which resulted in depletion of water in the soil profile compared with winter, during which most of the plants have slow growth rate. Among rainfall interception treatments, residual soil water content was lowest for the 60% rainfall interception, mainly because of the low amount of rainfall, which also resulted in the lowest aboveground biomass production (Magandana *et al.* 2020). The 60% rainfall interception treatment was characterized by more bare patches than other treatments, exposing the soil to unproductive water losses through evaporation. The 15% rainfall interception also resulted in low soil water content (SWC). The 15% rainfall interception had higher grass cover relative to the 30% and 60% rainfall interception treatments.

Forbs such as *Ipomea crassipes* have deep root systems and are able to extract water from deeper layers, leading to the proliferation of the grass species that have shallow root systems, thus exhausting the soil water content in the top 40 to 60 cm, soil layer causing low residual soil water content. Despite the lower rainfall received, the 30% rainfall interception treatment had relatively higher residual soil moisture content during summer than the 15% rainfall interception because of the relatively higher proportion of forbs in the former case (Magandana *et al.* 2020). The forbs have bigger leaves that cover the soil surface and prevent water loss through evaporation. According to Sun *et al.* (1997), root distributions of varied architecture allow plant species to co-exist and tolerate environmental stresses. Under water-limited conditions, deep rooted plants thrive better, dominating the plant species in the area (Collins & Bras 2007) by extracting water and nutrients from deeper soil layers. This was demonstrated by Dornbush & Wilsey (2010), who reported an increase in the number of new forbs species with greater soil profile depth.

Soil water content was affected by soil depth and resting period (Figures 2.3, 2.4). Soil water content increased linearly with soil depth, the top 20 cm layer having the lowest and the 40-60 cm layer the highest. This was mainly because of the exposure of the top 20 cm soil layer to high evapotranspiration losses relative to the deeper soil layers (Jiang *et al.* 2020). Residual

soil water content was relatively lower at the end of the summer season compared with that of autumn at 0–20 cm depth, mainly because of high evapotranspiration water losses during the summer season. Regardless of the season, resting the veld for 90 days generally resulted in lower residual soil water content than 70 days. This is attributed mainly to the maintenance of bigger canopy for 20 extra days, which resulted in higher water loss through evapotranspiration producing higher aboveground biomass (Magandana *et al.* 2020).

Climate change expressed through change in rainfall could affect the soil physical properties (Karmakar *et al.* 2016), chemical properties, including the amount and availability of nutrients (Zhi-yuan *et al.* 2013). Generally, rainfall interception did not affect soil total N, and total C, indicating that the amount of C and N added to the soil system through atmospheric deposition and plant residue recycling was in equilibrium with the amount of C losses through decomposition and N uptake by plants and losses through leaching and volatilisation. Zhou *et al.* (2013) reported similar findings, where drought did not affect total soil N and labile organic carbon. This indicates that there are long-term potential negative impacts of rainfall reduction on soil organic carbon and therefore, soil health. Similar to the findings from the current study, Sardans *et al.* (2008b) reported that warming and drought had no significant effect on soil pH.

Generally, soils in high rainfall areas are characterized by low-base cation concentration and low pH (Moslehi *et al.* 2019) because of the leaching of soluble ions (Atucha *et al.* 2013). The concentration of extractable residuals soil cations (Ca, K, Mg, Na, P) and anions (SO₄, NO₃) increased with increase in rainfall interception (Tables 2.3, 2.4). This is attributed to the decline in the leaching of ions because of the interception in the amount of water drained below the root zone (Sardans *et al.* (2008a). An increase in the concentration of residual soil NO₃ with the prevalence of drought was reported by Fry *et al.* (2018), which was in agreement with the current study. The interception in the leaching of cations and anions led to an increase in the soil electrical conductivity (EC) of higher rainfall reduction. Nonetheless, soils with high nutrient content and EC are more fertile than soils with low nutrients and EC (McKenzie *et al.* 2004).

2.5. Conclusion

Results from this study showed that an annual rainfall reduction of 60% could affect residual SWC negatively, thus affecting regrowth potential after defoliation by grazing or cutting of natural grasslands. The negative effect of rainfall interception on residual soil water content was more pronounced in summer than autumn. In contrast, rainfall interception was associated with higher extractable residual soil cations (Ca, K, Mg, Na, and P) and anions (SO₄

and NO_3) partly owing to the interception in leaching and partly because of reduced uptake of soil nutrients by plants. Rainfall interception, however, did not significantly affect soil pH, total N, and total C, indicating the minimal impact of climate change manifested in terms of rainfall interception on these parameters. Generally residual soil water content was higher at a deeper soil layer than the top layer, suggesting that plants with tap root system such as forbs capable of extracting water from the deeper soil layer will have competitive advantage to dominate the vegetation at 60% rainfall reduction, which was characterized by low residual soil water content than 0 or 30% rainfall reduction. Under 60% rainfall interception scenarios, the plants might not be able to grow fast and switch to reproductive stage. Resting the veld could also improve the soil chemical and physical properties..

Chapter 3

Annual net primary productivity of different functional groups as affected by different intensities of rainfall interception in the semiarid grasslands of the Gauteng province in South Africa

3.1 Abstract

Rainfall variability is expected to change the soil water regime, thereby impacting negatively on rangeland species composition, productivity and ecosystem services. The aim of this study was to assess the influence of different intensities of rainfall interception on vegetation annual net primary productivity (ANPP). Twenty 7×7 m experimental plots with different intensities of rainfall interception structures consisting of transparent acrylic bands were built on a natural grassland. The interspaces between acrylic bands varied in size to intercept different intensities of ambient rainfall (0, 15, 30 and 60%) as rainfall interception treatments, with each treatment being replicated five times in a complete randomised block design. A fixed 1 m^2 quadrat was marked at the centre of each plot and the annual net primary productivity (ANPP) within the quadrats was determined by harvesting the quadrat at the end of the growing season. Generally, compared with the control (ambient rainfall intensity) the overall grass ANPP ($P > 0.05$) showed resilience to lower and moderate intensities of (15 and 30%) rainfall interception, but at a severe intensity of rainfall interception (60%) the ANPP was significantly reduced. Compared with the control, the percentage contribution of grasses towards the overall ANPP increased at a lower intensity of rainfall interception (15%). In contrast, the percentage contribution of forbs towards the overall ANPP was reduced significantly at lower intensity of rainfall interception. Within the grass species, however, those grasses that decrease when the veld is undergrazed or overgrazed (decreaser grass species) showed resilience at lower intensity (15% and 30%) of rainfall interception, whereas at a severe intensity of rainfall interception the ANPP of decreaser grasses were significantly reduced from 1841 to 220 kg DM/ha. Those grasses that increase with undergrazing or overgrazing (increaser I or increaser II grass species) recorded a higher ANPP at moderate intensity of rainfall interception (30%) than at a higher intensity of rainfall interception, whereas the difference between 60% rainfall interception and 0% rainfall interception in terms of increaser grasses ANPP were not significant ($P > 0.05$) (650 kg DM.ha⁻¹). Up to 88% reduction in ANPP were recorded for decreaser grass species at severe intensity of rainfall interception compared with the control. The corresponding reduction in ANPP noted for increaser grasses was relatively less (up to 56% reduction in ANPP at 60% rainfall interception as opposed to 0% rainfall interception). Generally, the overall ANPP yield of the semi-arid grassland showed resilience

to a low intensity of rainfall interception (15% rainfall interception) and moderate intensity of rainfall interception (30% rainfall interception) partly because of a shift in the species composition of grasses from decreasers to increasers ecological groups, and because of a decrease and an increased contribution of forb functional groups at a lower and moderate intensity of rainfall interception, respectively.

Keywords: ANPP; decreasers; ecological status; forbs; grass

3.2. Introduction

Global climate models forecast an increase in frequency and climate extremes (IPCC, 2013). Those extremes included drought. Drought can be defined as a natural hazard, which is complex in nature and characterised by below-average rainfall beyond a given threshold over time, impacting society and ecosystems in different ways (Van Loon 2015; Tfwala *et al.* 2018). Drought is classified into four types, namely hydrological, socioeconomic, meteorological and agricultural. The focus of the current study is on meteorological drought, which occurs as a result of rainfall interception for a prolonged period (Dai 2011). There is evidence that change in rainfall alters natural resources such as tree and grass productivity (IPCC 2014; Knapp *et al.* 2015). Water availability also affects terrestrial species composition as some of these species have shifted their geographic occurrence and abundance as a result of changes in species interactions associated with climate change (IPCC 2014).

The forecast global increase in land surface temperatures is between 1.1 °C and 6.4 °C by the end of the century (Hui *et al.* 2018). This increase in temperatures is expected to affect rainfall amount and patterns, which will lead to more rainfall variability and the occurrence of extreme rainfall events (Huntington 2006). Rainfall variability will have a significant impact on soil moisture availability, which influences annual net primary productivity ANPP and ecosystem productivity (Knapp *et al.* 2015; Fay *et al.* 2003). Rainfall variability includes rainfall intensity (ratio of the total amount of rain falling during a given period to the duration of the period), duration (period during which continuous rainfall is observed) and frequency (number of times that rain occurs during a specified period of years). The study focused on the impact of rainfall intensity.

Climate change in the form of floods, storms and droughts has adverse socio-economic impacts on human and animal welfare, mainly through its effect on primary productivity and animal production and services from the grassland ecosystem (Huntington 2006). Developing countries such as South Africa with scarce resources for adaption and mitigation strategies are most likely to be affected by these threats (Manabe 2004). Extreme rainfall variability and events such as droughts are already evident from the reports of shifts in intra-annual rainfall patterns (Knapp *et al.* 2015). The major factor that controls the grassland ecosystem and structure globally is the climate (Fay *et al.* 2003), of which rainfall plays a major role in semi-arid and arid environments. Rainfall variability and events affect soil water content, which alters the primary productivity of grassland ecosystem in semi-arid and arid environments. Grasslands are likely to respond rapidly and strongly to variability and extreme rainfalls, as this determines soil water content (Volk *et al.* 2000).

The sustainability and productivity of natural grasslands depend mainly on rainfall and temperature, and these will be affected by forecast warmer temperatures and interception in rainfall (IPCC 2007; Volaire *et al.* 2014). When severe reduction in rainfall is accompanied by higher temperatures, it is likely to lead to more frequent and intense droughts (Trnka *et al.* 2011), which will lead to plant deterioration that will result in grassland degradation (Ciais *et al.* 2005). Perennial forage species are often expected to grow under reduced rainfall (Volair *et al.* 2014). However, only plants with drought survival strategies will adapt best under increasing RI conditions (Lelievre *et al.* 2011). It is argued that grass species and genotypes use different strategies to tolerate and avoid drought stress, and as a result plant responses to drought are poorly understood and described (Soussana *et al.* 2010). Some ecological groups of grasses decrease with undergrazing or overgrazing (referred to as decreasers), whereas others increase with undergrazing or overgrazing (increasers).

The intensity of aboveground biomass harvested by animals affects the root size. Because decreasers are frequently consumed, they may have less vigour and lower root biomass, which makes them disadvantaged in extracting soil water compared with increaser grasses that are less grazed and thus may have well-developed root systems. It is reported that drought also reduces decreasers and increases increasers (Magandana *et al.* 2020). Increasers use rainfall more efficiently than decreasers because of well-established leaf areas as a result of lower defoliation frequency and intensity associated to their lower palatability, whereas decreaser species, often highly palatable, are expected to have less leaf area because of more frequent and intensive defoliations of the leaves. Hence, increasers are considered more tolerant to grazing than decreasers.

Drought may lead to physiological and morphological plant modifications (Kleine *et al.* 2017). However, most genotypes that survive in the most arid regions are the ones that become dormant in winter (Norton *et al.* 2008; Norton *et al.* 2009). Under limited resources, the growth of individual plants is also affected by the neighbouring plants (Gioria & Osborne 2014). Thus, resource availability will regulate the plant community and this is the main contributing factor to the abundance of forbs during and after a drought (Gioria and Osborne 2014).

Climate change has triggered many studies, which include those that determine the impact of reduced rainfall on rangeland productivity. Rainfall in South Africa will decline by about 15% by the end of the 21st century (Jury 2013). Few studies have been conducted in

Africa in general and South Africa in particular that show the impact of this amount of rainfall interception on species composition, primary productivity and overall productivity of the grassland ecosystem. The increasing rainfall interception in South Africa remains poorly described, although there is evidence that the vegetation is changing owing to climate change (Tfwala *et al.* 2018; Magandana *et al.* 2020). In particular, it is important to evaluate the long-term effect of intensity of rainfall interception on semi-arid grasslands, as there is less information on this topic at regional scale in South Africa.

This study complements the study reported by Magandana *et al.* (2020) on the same grassland that evaluated the impact of intensity of rainfall interception and resting period on rangeland productivity over the different seasons. Unlike Magandana *et al.* (2020), this study investigates how intensity of rainfall interception will affect the overall annual net primary productivity and the ANPP of different ecological and functional groups in the grassland. It generates some evidence on how the forecast reduction in rainfall will affect South African grassland productivity, species composition in terms of ecological grouping and functional groups, and how farmers should manage their grasslands in the future under different intensities of rainfall interceptions.

3.3. Materials and methods

3.3.1. Site description

The study was conducted in a semi-arid natural grassland at Hatfield Experimental Farm, University of Pretoria, (Figure 5.1). The farm is situated at an altitude of 1372 m above sea level. The coordinates of the study sites are 25°45′ S and 28°16′ E. The farm is situated in a summer rainfall area with a long-term annual rainfall of 674 mm. The soil is categorized as sandy loam with 32.1 – 34.3% clay (Soil Classification Working Group) and a pH of 5.1. The soil is non-calcareous with a homogenous red colour, weak structure and is of Hutton form (Soil classification working group 1991). The study site has not been grazed for more than 65 years.

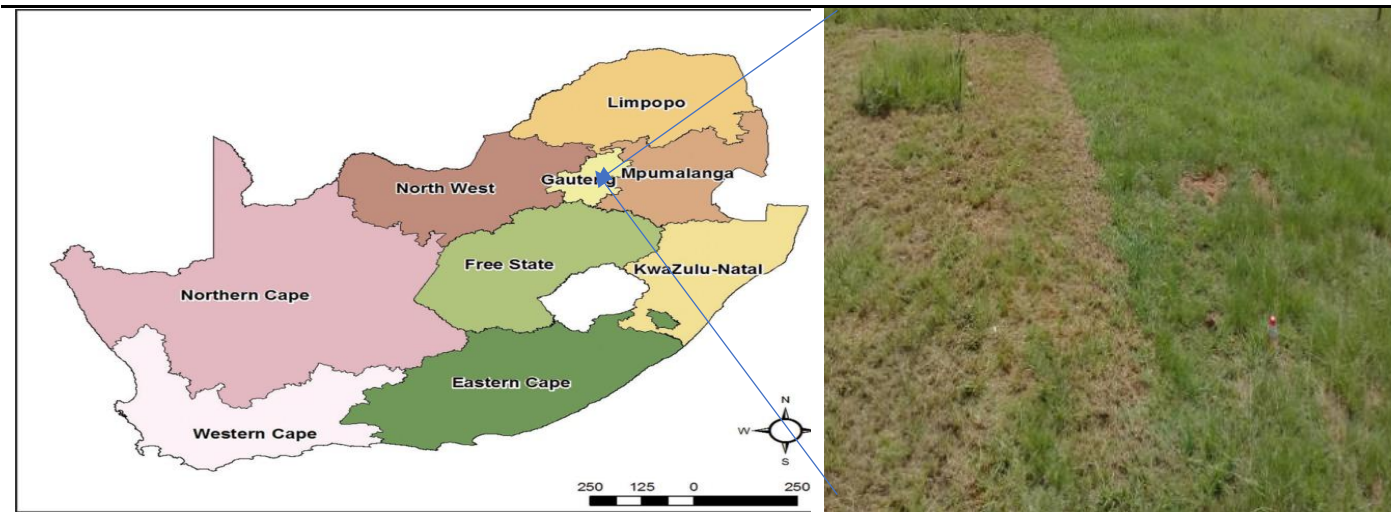


Figure 3.1 South African map showing study site and the illustration of the methods (<https://geology.com>).

3.3.2. Experimental design and data collection

The long-term experimental rainout shelters have been in existence since 2013 while we started collecting data from 2016 to 2019 (Figure 3.2). Twenty 7×7 m experimental structures (plots) consisting of transparent acrylic bands were built on a natural grassland (Appendix A). Rainfall interception was conducted at four intensities, namely (0%, 15%, 30% and 60%) using the rainout shelters for each treatment that were replicated five times in a complete randomised block design (Figure 3.2). Different intensity of rainfall interception was achieved by intercepting the ambient rainfall with a number of acrylic bands fixed per rainout structure. A fixed 1 m^2 quadrat (Figure 3.2a) was marked at the centre of each plot and the ANPP within the quadrats was harvested once at the end of the growing season every year (year 1 and year 2).

The bands were constructed with a longitudinal plate of 120° angle at the top and a mean height of 1 m at the lowest sides of the shelter. A 25 cm ditch was excavated along the structures to avoid water runoff into the plots. Water was collected from the acrylic material and channelled through gutters away from the neighbouring plots. The vegetation was cleared at the height of 5 cm above the ground at the beginning of the experiment for all the plots in November 2016. This was to ensure that the experiment was started at the same growth height. The ANPP samples harvested to determine annual net primary productivity (ANPP) were taken in November 2017 and 2018. A 1×1 m quadrat of ANPP was harvested from each plot. Plants present in each quadrat were identified and counted to determine species composition and plant density.

The harvested ANPP samples were oven-dried to a constant weight at 60°C for 72 hours (Soil Classification Working Group 1991). Plants were grouped in functional groups (grasses

and forbs). Grasses were further grouped into ecological status: 1) decreasers- those grasses abundant in a veld that is in good condition but decrease when the veld is undergrazed or overgrazed; and 2) increasers those grasses that increase because of undergrazing (termed increaser I) or overgrazed (termed increaser II). The former include mostly pioneer and subclimax species, and they are also common in lower rainfall areas (Van Oudtshoorn 2012). This was because grass ecological groups respond in different ways to level of grazing (Van Oudtshoorn 2012) and rainfall (Talore 2015). The classification into functional status and ecological status was done before drying the samples. Rainfall was recorded after every rainfall event using a rain gauge (Figure 3.3). Rain use efficiency (RUE) was calculated as follows; $RUE (kg \cdot ha^{-1} \text{ per mm rainwater}) = Yield (kg \cdot ha^{-1}) \text{ divided by cumulative rainfall (mm)}$ from the beginning of the sampling period until the harvest (Sharma *et al.* 2013)



A



B



C



D

Figure 3.2 Experimental design: (A) 0% rainfall interception (no interception), (B) 15% rainfall interception, (C) 30% rainfall interception and (D) 60% rainfall interception

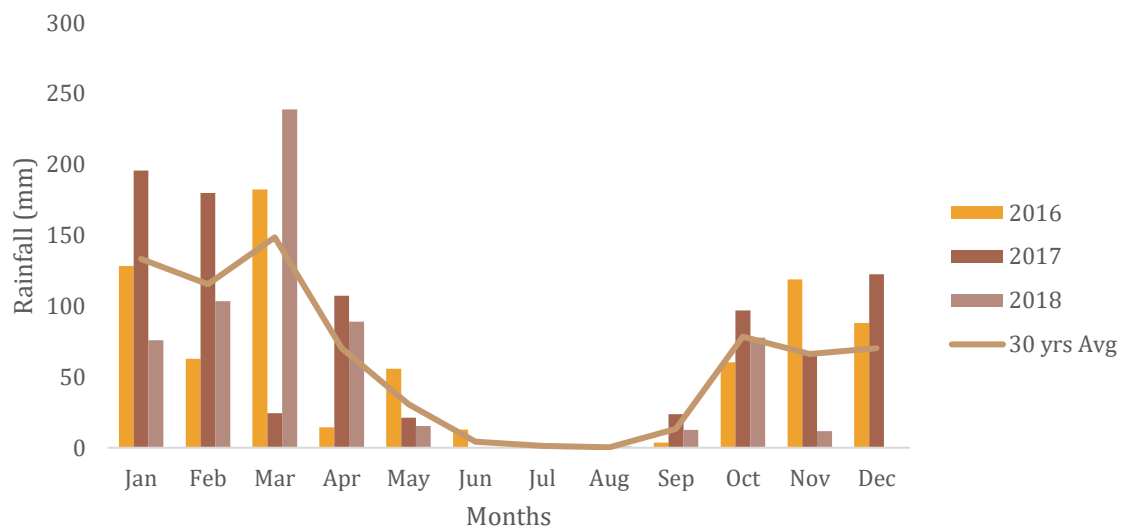


Figure 3.3 Rainfall distribution for each month of the year

3.3.3. Statistical analyses

The data on the ANPP were subjected to the general linear model (PROC GLM) procedure of (SAS 2008) to determine the main effects of the rainfall interception intensities and the years as a repeated measure on overall, species functional (grasses and forbs) and ecological (decreasers and increasers) group ANPPs. The blocks were added as a random factor to the model. However, they were not reported in the results section because there were no significant interactions between rainfall interception and block. Data were tested for normality and homoscedasticity using the Shapiro–Wilk test. Where the factors showed a significant effect on the ANPP, Tukey’s test was used for mean separation at a significance level of 5%. The

results were reported as a mean $\pm$ standard error. Principal component analysis (PCA) was used to conduct ordination between treatments and grass species. Species that were identified in various treatments were used for PCA. Only grasses that were common in all of the treatments were included in the PCA, whereas forbs were not included, because they were not identified at species level. All the rainfall interception intensities were included in the analysis. The ordination analysis was executed using Past3 software.

3.4. Results

Increaser grasses such as *Eragrostis curvula*, *Cynodon dactylon* and *Heteropogon contortus* occurred more at 30% and 60% rainfall interception (Table 3.1). On the other hand, decreaser grass species such as *Digitaria eriantha*, *Setaria sphacelata*, *Setaria nigrirostris* and *Themeda triandra* occurred more at 0%, 15% and 30% rainfall interception. Moreover, forbs such as *Nidorella resedifolia* and *Ipomoea crassipes* occurred mostly at 30% and 60% RI, whereas *Elephantorrhiza elephantina*, a shrub, was more common at 30% rainfall interception.

Table 3.1 Ecological status, presence or absence and level of occurrence of grass/forb species in plots subjected to various intensities of rainfall interception at the University of Pretoria Experimental Farm

Scientific Names	Functional Group	Life Form	Growth Form	Ecological Status	Grazing Value	Intensity of Rainfall Interception (%)			
						0	15	30	60
<i>Aristida congesta</i>	Grass	WP	Tufted	Increaser II	Low			+	++
<i>Brachiaria serrata</i>	Grass	P	Tufted	Decreaser	Ave			+	
<i>Melinis repens</i>	Grass	P	Tufted	Increaser II	Low		+	+	
<i>Cynodon dactylon</i>	Grass	P	Creeping	Increaser II	High		+	++++	+++++
<i>Digitaria eriantha</i>	Grass	P	Tufted	Decreaser	High	+++++	+++++	++++	+++
<i>Elephantorrhiza elephantina</i>	Forb	P	—	Shrub	Low		+	++++	
<i>Rhynchosia monophylla</i>	Forb	P	—	Increaser II	Low	+			
<i>Eragrostis curvula</i>	Grass	P	Tufted	Increaser II	Ave	+++	++++	+++++	+++++
<i>Heteropogon contortus</i>	Grass	P	Tufted	Increaser II	Ave	+++	+	+++	+++++
<i>Hyparrhenia hirta</i>	Grass	P	Tufted	Increaser I	Low			+	
<i>Hypoxis hemerocallida</i>	Forb	A	-	Invader	Low	+			+
<i>Ipomoea crassipes</i>	Forb	A	-	Invader	Low	++	+	++++	+++++
<i>Nidorella resedifolia</i>	Forb	A	-	Invader	Low	++	++	++++	++++
<i>Setaria nigrirostris</i>	Grass	P	Tufted	Increaser II	Low	++++	++	+++++	
<i>Setaria sphacelata</i>	Grass	P	Tufted	Decreaser	High	+++++	+++++	+++++	++
<i>Themeda triandra</i>	Grass	P	Tufted	Decreaser	High	++++	+	++++	
<i>Verbena officinalis</i>	Forb	A	-	Invader	Low				++

√: presence, WP: weak perennial, P: perennial, Ave: average, +: appearing in one of the five replicates, ++: appearing in two of the five replicates, +++: appearing in three of the five replicates, ++++: appearing in four of the five replicates, +++++: appearing in all five replicates.

In both years, control plots (Y1RI0 and Y2RI0) were on the fourth quadrat of the principal component analysis (PCA) in terms of densities per square metre (Figure 3.4). This meant that the control plots responded the same in the two years. Meanwhile, the 15% RI plots (Y1RI15 and Y2RI15) were on the first quadrat in both years. This means that there were no

differences in these plots in the two years. However, 30% RI plots (Y1RI30 and Y2RI30) are on different quadrats. This means that there were differences in way these plots were affected between 2017 and 2018. Moreover, 60% RI plots (Y1RI60 and Y2RI60) were on different quadrats. The 60% RI did not respond the same way in 2017 and 2018. The 15% RI favoured *E. curvula*, *D. eriantha* and *H. contortus*. In 2017, both Y1RI30 and Y1RI60 favoured *I. crassipes*, *E. elephantina*, *N. resedifolia*, *B. pilosa* and total forbs densities, whereas 60% RI favoured *C. dactylon* in 2018. The 0% RI favoured decreaser grass species and the total densities.

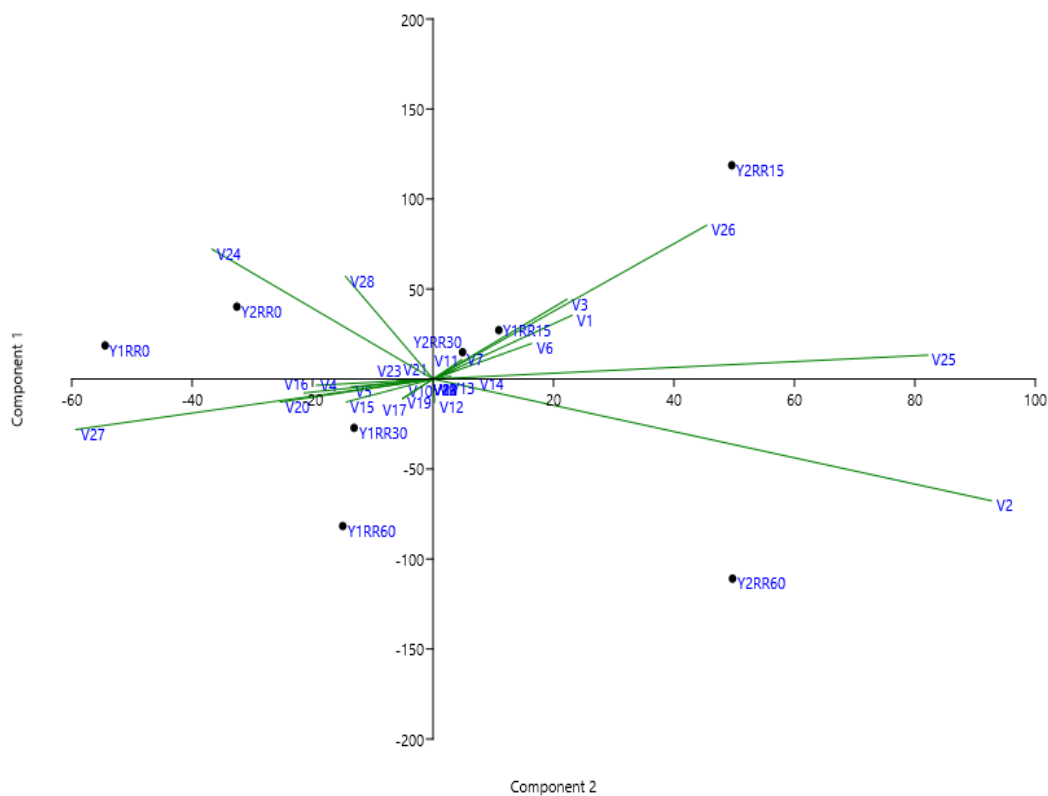


Figure 3.4 Grass and forb species densities per square meter over two years (2017 and 2018)

V1: *Eragrostis curvula*, V2: *Cynodon dactylon*, V3: *Digitaria eriantha*, V4: *Setaria nigrirostris*, V5: *Themeda triandra*, V6: *Heteropogon contortus*, V7: *Setaria sphacelata*, V8: *Eragrostis barbinodis*, V9: *Melinis repens*, V10: *Brachiaria seriata*, V11: *Aristida congesta*, V12: *Ipomoea crassipes*, V13: *Elephantorihiza elephantina*, V14: *Rhynchosia monophylla*, V15: *Bryophyllum delagoense*, V16: *Hypoxis hemerocallida*, V17: *Nidorella resedifolia*, V18: *Conyza fleabane*, V19: *Verbena officinalis*, V20: *Bidens pilosa*, V21: *Cyperus* species, V22: *Urochloa mosambicensis*, V23: *Solanum* species, V24: decreasers, V25: increasers, V26: forbs, V27: total density, Y1RI0 and Y2RI0: 0% RI in 2017 and

2018, respectively, Y1RI15 and Y2RI15: 15% RI in 2017 and 2018, respectively, Y1RI30 and Y2RI30: 30% RI in 2017 and 2018, respectively, Y1RI60 and Y2RI60: 60% RI in 2017 and 2018, respectively

RI: rainfall interception

The two 15% RI treatments were close together in terms of annual net primary productivity (ANPP) (Figure 3.5). The two 30% RI treatments were close to each other. Meanwhile, the two 60% RI were in the same place. This meant that the treatments behaved the same way in both years. *D. eriantha* and total decreaseers were closely correlated to 15% rainfall interception. On the other hand, *C. dactylon* was closely correlated with 60% rainfall interception. Forbs and total increaser ANPP were closely correlated with 30% rainfall interception. The 30% RI was grouped together and correlated with forbs in terms of occurrences (Figure 3.6). *Eragrostis curvula*, *C. dactylon*, and total increasers were closely correlated with 60% rainfall interception. *Setaria sphacelate*, *D. eriantha* and total decreaseers were closely correlated with 15% rainfall interception. The 0% RI favoured *Setaria nigrirostris*, *Heteropogon contortus* and *Melinis repens*.

Year and RI interaction had no significant effect on overall, forbs, decreaseer, and overall grass ANPP after data were log transformed (Table 3.2). Year had no significant effect amongst the same treatments. However, RI had a significant effect on overall, forbs, decreaseer, and overall grass ANPP. Moreover, year had a significant effect on forbs, increaser and overall grass ANPP, whereas it had no significant effect on overall and decreaseer ANPP. The 60% RI resulted in low ($p < 0.05$) overall ANPP, decreaseer, increaser and overall grass ANPP. Overall ANPP, decreaseer and overall grass ANPP were resilient up to 30% RI after which they declined at 60% RI. Meanwhile, unlike grasses, forbs were lower ($p < 0.05$) at 15% RI, whereas there was no significant difference between 0%, 30% and 60% RI. Although there was no significant difference between 0%, 15% and 60% on increaser grass ANPP, 60% RI had a low ($p < 0.05$) ANPP compared with 30% RI. Forbs ANPP was higher ($p < 0.05$) in 2018 than 2017. On the other hand, unlike forbs, increaser grass and overall grass ANPP was higher ($p < 0.05$) in 2017 than 2018.

Year and RI had no significant interaction effect on forbs, decreaseers, increasers and overall grass percentage contribution on ANPP (Table 3.3). However, year and RI had a significant effect on forbs and overall grass percentage contribution on ANPP. Forbs were significantly lower at 15% RI than 0, 30 and 60% RI. Year 2018 resulted in high ($p < 0.05$) forbs proportion than 2017. On the other hand, unlike forbs overall, grass percentage

contribution was higher ($p < 0.05$) at 15% than 0, 30 and 60% RI, whereas year 2017 had a high ($p < 0.05$) overall grass percentage than 2018. Meanwhile, year and RI had no significant effect on ecological status of the grass (decreasers and increasers).

Year and RI interaction had no significant effect on rain use efficiency (RUE) (Figure 3.7). However, RI had a significant effect on RUE. Meanwhile, year had no significant effect on RUE. The 30% RI resulted in a high ($p < 0.05$) RUE than 15 and 60% RI, whereas there was no significant difference between 0 and 30% RI. Rainfall interception and year had no significant interaction effect on all grass species ANPP (Table 3.4). Year had no significant effect on all grass species ANPP. However, RI had a significant effect on *C. dactylon* and *S. nigrirostris*, whereas it had no significant effect on other grass species. *Cynodon dactylon* was significantly higher at 60% RI compared with other treatments. The 15% RI resulted in a significantly low *S. nigrirostris* compared with 0% RI, whereas there was no significant difference between 30 and 15% RI.

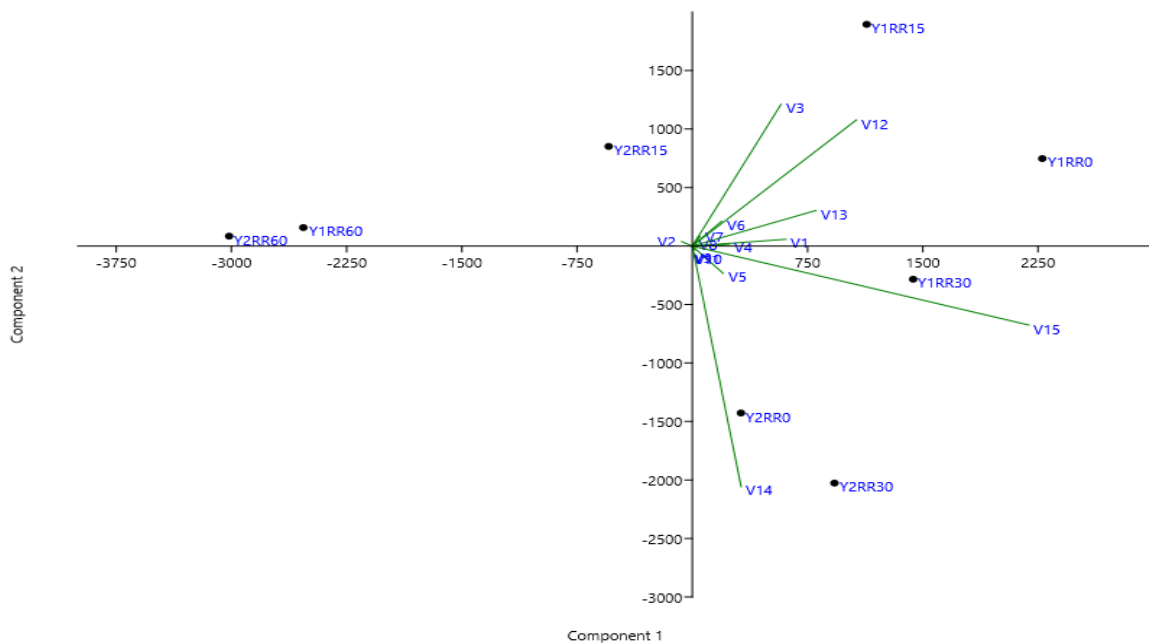


Figure 3.5 Principal component analysis (PCA) of ANPP of various species and functional groups in 2017 and 2018: V1: *Eragrostis curvula*, V2: *Cynodon dactylon*, V3: *Digitaria eriantha*, V4: *Setaria nigrirostris*, V5: *Themeda triandra*, V6= *Heteropogon contortus*, V7: *Setaria sphacelata*, V8: *Eragrostis barbinodis*, V9: *Melinis repens*, V10: *Brachiaria seriata*, V11: *Aritida congesta*, V12: decreaser, V13: increaser, V14: forbs, V15: total ANPP, Y1RI0 and Y2RI0: 0% RI in 2017 and 2018, respectively, Y1RI15 and Y2RI15: 15% RI in 2017 and 2018, respectively, Y1RI30

and Y2RI30: 30% RI in 2017 and 2018, respectively, Y1RI60 and Y2RI60: 60% RI in 2017 and 2018, respectively

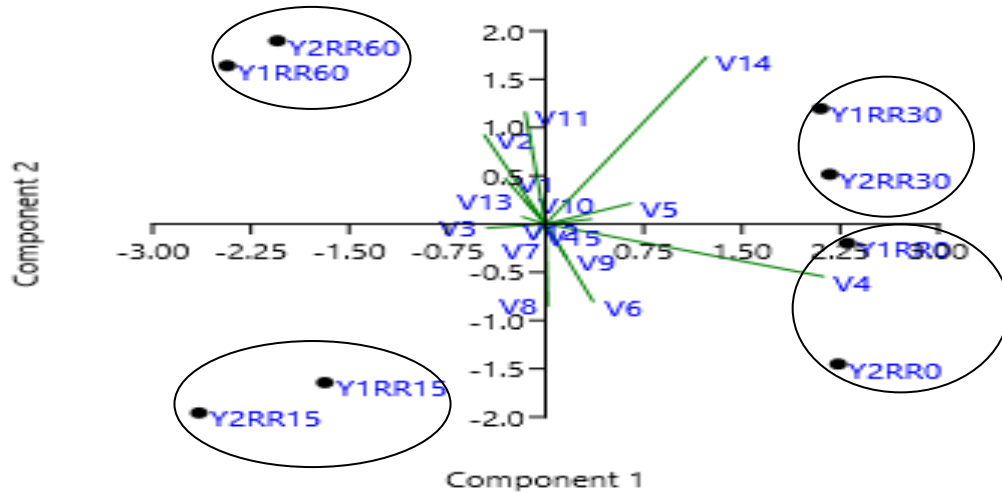


Figure 3.6 PCA analysis of occurrence of species and functional groups in various plots subjected to different intensities of RI: V1 =*Eragrostis curvula*, V2: *Cynodon dactylon*, V3: *Digitaria eriantha*, V4: *Setaria nigrirostis*, V5: *Themeda triandra*, V6: *Heteropogon contortus*, V7: *Setaria sphacelata*, V8: *Eragrostis barbinodis*, V9: *Melinis repens*, V10: *Brachiaria serrata*, V11: *Aritida congesta*, V12: decreaser; V13: increaser; V14: forbs. Y1RI0 and Y2RI0: 0% RI in 2017 and 2018, respectively, Y1RI15 and Y2RI15: 15% RI in 2017 and 2018, respectively, Y1RI30 and Y2RI30: 30% RI in 2017 and 2018, respectively, Y1RI60 and Y2RI60: 60% RI in 2017 and 2018, respectively.

Table 3.2 Annual net primary productivity of different functional groups as affected by different intensity of rainfall interception in Pretoria

Rain Interception	Annual Net Primary Productivity (kg DM/ha)				
	Overall ANPP	Forbs ANPP	Grass ANPP		
			Decreaser Grass ANPP	Increaser Grass ANPP	Overall Grass ANPP
0%	4979 ^a	1666 ^a	1841 ^a	1472 ^{ab}	3312 ^a
15%	3761 ^a	316 ^b	2029 ^a	1416 ^{ab}	3445 ^a
30%	5029 ^a	2066 ^a	1147 ^a	1816 ^a	2963 ^a
60%	1716 ^b	846 ^a	220 ^b	650 ^b	869 ^b
S.E	658.8	312.75	500.06	327.05	562.38
<i>P</i> -value	0.007	<0.0001	0.055	0.060	0.002
Year					
2017	4184	760 ^b	1673	1752 ^a	3424 ^a
2018	3558	1688 ^a	946	925 ^b	1870 ^b
S.E	465.9	221.1	353.6	231.3	397.7
<i>P</i> -value	0.349	0.046	0.461	0.023	0.019

Different small letter superscripts along the same column were significantly different. S.E: Standard error.

Table 3.3 Percentage contribution of different functional groups in terms of annual primary productivity as affected by intensity of rainfall interception in Pretoria

Rainfall Interception	% Contribution in Terms of ANPP			
	Grass ANPP			
	Forbs	Decreaser	Increaser	Overall Grass
0%	36 ^a	33	31	64 ^b
15%	6 ^b	44	50	94 ^a
30%	42 ^a	22	36	58 ^b
60%	48 ^a	17	35	52 ^b
S.E	7.4	8.3	8.8	7.0
<i>P</i> -value	<0.0001	0.254	0.534	0.001
Year				
2017	23 ^b	32	45	77 ^a
2018	43 ^a	26	31	57 ^b
S.E	5.2	5.8	6.2	5.1
<i>P</i> -value	0.022	0.764	0.088	0.004

Different small letter superscripts along the same column were significantly different.

S.E: Standard error.

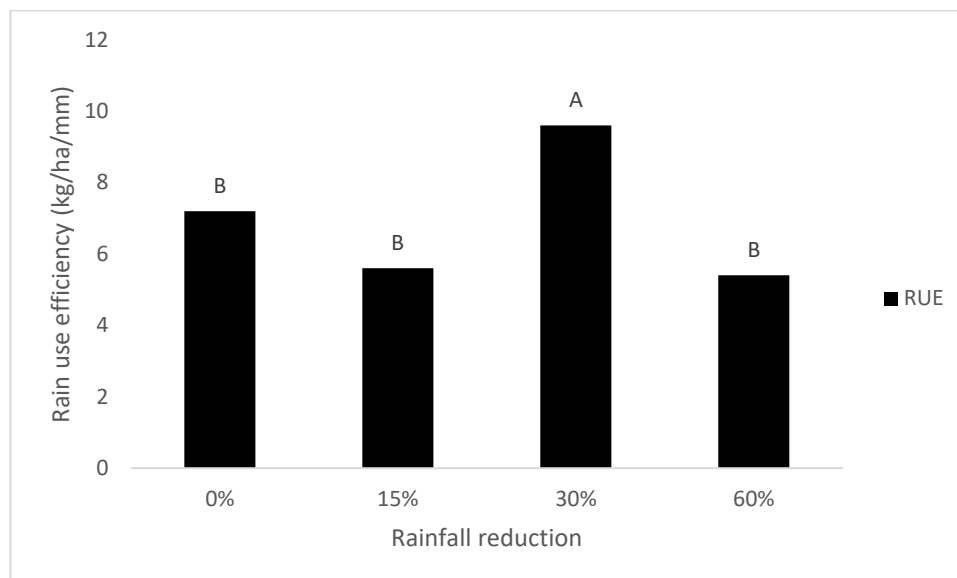


Figure 3.7 Rain use efficiency of the semi-arid grassland as affected by different intensities of rainfall interception in Pretoria

Table 3.4 Percentage most common species contribution on grass annual net primary productivity of the semi-arid grassland as affected by different intensity of rainfall interception in Pretoria.

Grass Species (%)							
Rainfall Interception (%)	<i>Eragrostis curvula</i> Log	<i>Cynodon dactylon</i> Sqrt	<i>Heteropogon contortus</i>	<i>Digitaria eriantha</i> Log	<i>Setaria nigrirostris</i> Log	<i>Themeda triandra</i>	<i>Setaria spacelata</i>
0	37.9	0.2 ^b	7.7	23.0	12.3 ^a	0.2	0.9
15	37.2	1.2 ^b	9.7	40.6	4.5 ^{bc}	0.1	1.7
30	54.5	0.9 ^b	5.5	16.0	5.1 ^{ab}	0.2	0.8
60	40.8	18.7 ^a	1.5	30.3	0 ^c	0	3.4
S.E	11.64	4.3	3.18	8.92	3.47	0.06	1.41
P-value	0.2206	0.0253	0.3880	0.4242	0.0036	0.1248	0.5684
Year							
2017	48.6	5.5	5.5	28.4	4.6	0.1	1.2
2018	36.6	5.0	6.8	26.6	6.3	0.1	2.1
S.E	8.23	3.04	2.25	6.31	2.45	0.04	1.03
P-value	0.5852	0.9586	0.8621	0.5919	0.9152	0.9335	0.5269

Different small letter superscripts along the same column were significantly different.

S.E: Standard error.

3.5. Discussion

Rainfall interception effects dominated parameter responses with 2017 having higher ANPP than 2018. This response was as a result of reduced rainfall which resulted in reduced ANPP. The results concur with those reported by (Hoover *et al.* (2014) who reported that imposed drought reduced ANPP below the fifth percentile of the historical contribution of ANPP values for a particular site. Previous study on the ecosystem by Nippert and Knapp (2007) showed that forbs mainly rely on deep soil moisture to avoid water stress during dry periods; on the other hand, grasses rely mainly on shallow soil moisture to tolerate dry periods.

Rainfall interception owing to climate change has a potential to affect species representation of the semi-arid grassland (Table 3.1). The results of this study show that reduced rainfall benefited increaser grass species and invaders as they dominated at 30% and 60% RI. These results concur with those reported by Prev  y and Seastedt (2015), who reported that change in rainfall patterns because of climate change affects population dynamics of invasive species. In this study, we show how effects of climate change in the form of reduced rainfall will affect the species composition of the semi-arid grassland. It can be said that reduced rainfall is the major driver of the vegetation change, especially when other species are reduced.

Plant densities were higher at 0 and 15% compared with 30 and 60% rainfall interception (Figure 3.4). Plant densities were reduced with the increase in rainfall interception. This means that more soil will be exposed to water and wind erosion with less soil cover. This is as a result of reduced densities of the decreaser grass species through reduced rainfall, which is supported by Gilo and Kelkay (2017), who reported that the major factor contributing to decline in the abundance of highly desirable grass species is drought. This is also due to low germination rate from the soil seedbank and plants that die at seedling stage due to wilting. Reduced rainfall paves a way for invaders and some undesirable plants to dominate over highly desirable grass species.

The PCA also showed a certain trend that certain grasses and forbs behaved in a certain way (Figure 3.5). *Digitaria eriantha* and all the decreasers that are highly desirable grass species correlated with 0, 15 and 30% RI, whereas *C. dactylon* correlated with 60% rainfall reduction. The forbs and total ANPP correlated with 30% rainfall reduction. The *D. eriantha* is less resistant to water stress; hence, it only performed well at low rainfall interceptions and began to decline beyond this treatment. It can be said that other grasses

and forbs were suppressed by these decreaser grasses at 15% rainfall reduction, whereas they gained advantage at 30% rainfall interception after decreaser declined as a result of rainfall interception. Forbs gained advantage because of the deeper root system that allows them to access water from the deeper layers of the soil compared with some of the tropical grasses that are able to close stomata to reduce water loss through transpiration.

In this study, semi-arid grassland ecosystem was exposed to four intensities of rainfall interception to simulate different levels of available moisture to the soil from rainfall. The rainfall interception effect on ANPP was extreme under 60% rainfall reduction. The results show that reduced rainfall has a significant effect on the overall ANPP production only when it is severe. Rainfall interception had no significant effect on overall ANPP at moderate drought simulations (15 and 30% rainfall reduction) in both years.

Overall ANPP includes all the grasses and forbs that were harvested at the plots. In 2017, there was more rainfall and higher ANPP than in 2018. These results concur with those reported by (Greco and Cavagnaro 2002; Heitschmidt *et al.* 2005; Power *et al.* 2016; Van Der Weijde *et al.* 2017) who reported that rainfall interception reduces biomass yield. The fact that differences between the overall ANPP for 0, 15 and 30% rainfall interception were not significantly different, it means that the overall ANPP could tolerate up to 30% rainfall reduction, after which it declined. The 0% rainfall interception had the highest overall ANPP, whereas 60% rainfall interception had the lowest overall ANPP. The overall ANPP decreased by 74% at 60% rainfall interception compared with 0% rainfall interception ANPP. These results were a result of reduced rainfall because of increased intensity of rainfall interception. Although there was no significant difference between 0, 15 and 30% rainfall reduction, overall ANPP decreased with increase in rainfall reduction. Therefore, it can be said that decreased rainfall leads to decreased ANPP production as it was the case with the current results. It can also be said that most ANPP was accumulated in summer (December, January and February) when the rainfall was higher than the other seasons (Figure 3.3).

Grass ANPP was significantly lower under 60% rainfall interception. Although there was no significant difference between 0, 15 and 30% rainfall reduction, grass ANPP decreased linearly with the increase in rainfall interception. The grass ANPP decreased by 74% at 60% rainfall interception (Table 3.2). These results concur with those reported by Power *et al.* (2016), who suggested that ANPP is significantly affected by rainfall

scenarios. Previous studies have established a close relationship between plant growth and rainfall amount (Sala *et al.* 1988; Hsu *et al.* 2012; Southon *et al.* 2012), whereas Koerner and Collins (2014b) found no significant effect of drought simulation on ANPP productivity. The reason for the decrease in grass ANPP productivity is because the grasses prefer to extract soil moisture from top layers of soils because of their shallow root system (Nippert & Knapp 2007). The shallow root system of the grasses limits the uptake of resources such as water, nitrogen and phosphorus (Lenhart *et al.* 2015), which are necessary for plant growth that leads to reduced grass ANPP.

Unlike grasses, forbs increased with the decrease in rainfall as they had higher ANPP in 2018 than 2017 (Table 3.2). These results concur with those that were reported by (Briggs and Knapp 2001; Nippert *et al.* 2006) who reported that forbs productivity does not correlated with the rainfall amount within years. In the current study, forbs responded contrary to grasses. The ANPP for the forbs was also increased because there is less competition with the grasses as there are fewer grasses with less rainfall; this was the case with previous studies (Briggs & Knapp 2001; Nippert *et al.* 2006). It could be argued that the contradictory response of forbs and grasses to reduced rainfall is because of contrasting root systems and competitive interactions (Gherardi & Sala 2015).

The deeper root system allows forbs to access water and soil nutrients that are in the deeper layers of the soil, whereas shallow root system of the grasses only allows grasses to access water available in the top layer of the soil (Sala *et al.* 1992; Jackson *et al.* 1996; Weltzin & McPherson 2000). Therefore, the response of the two plant types (grasses and forbs) to resource availability determines distribution (Sala *et al.* 1992). Grasses eventually die in the absence of water and nutrients, giving space to more forbs to grow. A large volume of soil water that percolates from the topsoil layer is exploited by the deep root system of the forbs, whereas the grasses exploited the smaller volume of soil water accessible in the topsoil layers (Gherardi & Sala 2015). This explains how forbs are likely to be less affected by higher intensity of reduced soil moisture as opposed to grasses. The ANPP of the forbs is enhanced by the increased pools of resources that percolate deep into deeper layers of the soil, which are not available to shallow roots of grasses (Sala *et al.* 1989). The ANPP of the forbs under 60% rainfall interception decreased by 49% compared with 0% rainfall reduction, whereas that of grasses decreased by 74% at 60% rainfall interception compared with 0% rainfall reduction.

Our results showed that rainfall interception has a negative impact on the ANPP of common grass species in both years. All the grasses at the site were perennial C₄ pathway

species, whereas the forbs were C₃ pathway species. The *S. nigrirostris* ANPP percentage contribution was highest at 0% rainfall reduction, *D. eriantha* at 15% rainfall reduction, *E. curvula* at 30% whereas that of *C. dactylon* was highest at 60% rainfall interception (Table 3.4). Both *D. eriantha* and *S. nigrirostris* grass species are highly palatable decreaser grass species and they decreased with the increase in rainfall reduction, with 60% rainfall interception having the lowest ANPP. The *D. eriantha* is a non-drought tolerant grass species that is also adapted to a wide range of soil types (Moore *et al.* 2006). The increase in rainfall interception led to decreased soil moisture, which eventually led to decreased percentage contribution of most palatable grass species. Moreover, *E. curvula* is tolerant to drought and is also tolerant of soil acidity (Van den Berg & Zeng 2006). For this reason, the University of Pretoria experimental farm uses *E. curvula* because of its adaptability to the area and superior palatability to animals.

These grass species contributed most ANPP in the overall and grass ANPP. Grass leaf and stem size are affected by moisture availability and when moisture is limited morphological development of organs gets affected negatively (Fernández and Reynolds 2000). According to the trade-off hypothesis, species with a wide range of morphological characteristics differ largely in drought tolerance, with fast-growing species being very susceptible to low moisture content (Snyman & du Preez 2005). According to Snyman and Van Rensburg (1990), variability in rainfall overrides grazing in grass species change in semi-arid regions. Change in rainfall has a reflective effect on changes in grass ANPP. Other common grass species that contributed into grass ANPP were *Heteropogon contortus*, *Setaria sphacelata*, *Melinis repens*, *Brachiaria serrata* and *Aristida congesta*. However, these species did not constitute much of the ANPP.

Decreaser grass species contributed higher ANPP in 0 and 15% rainfall interception compared with increaser, whereas increasers had higher ANPP under 30% rainfall interception than decreaser grass species. Decreaser grass species (*D. eriantha*, *T. triandra*, *B. serrata*, *S. nigrirostris* and *S. sphacelata*) were fewer than increaser grass species (*A. congesta*, *C. dactylon*, *E. barbinodis*, *E. curvula*, *H. contortus* and *M. repens*). However, decreasers contributed more ANPP than increasers under higher soil moisture. Increaser grass species use water more efficiently than decreaser species (Xu & Zhou 2011), thereby leading to more ANPP under less soil moisture. It can be argued that decreaser grass species require more water to survive than increaser grass species. *Cynodon dactylon* is a rhizomatous grass species with more roots and shoots coming from

the nodes of the rhizomes compared with other perennial tufted grasses (Moore *et al.* 2006), which increase the surface area to absorb more soil water and nutrients.

A total of 840 mm of rainfall was received in the 2017 growing period, whereas 749 mm was received in 2018. The reduced rainfall will not only reduce grass production in grasslands, but also affect livestock and wildlife production as these animals rely on these natural resources to survive. Reduction in rainfall will lead to change in species composition and deterioration in grassland productivity that will ultimately lead to a reduction in wildlife and livestock production. Reduced grass cover could lead to more soil erosion, which could lead to land degradation and less vegetation for grazing animals. Less soil cover can also lead to poor water retention as less grass cover leads to more bare patches and more water runoff.

3.6. Conclusion

Overall, reduced rainfall had a significant negative impact on ANPP at 60% rainfall reduction. Reduced rainfall significantly affected grass ANPP more than forbs ANPP. Forbs have a deep root system that allows them to access water and nutrients from the deeper layers of the soil, which gives them advantage over grasses with shallow root system. From this study, we can say that *E. curvula* requires less water to produce dry matter than *D. eriantha*. Livestock farmers who rely on natural grazing land should promote growth of grasses such as *E. curvula* to produce enough grass during periods of low to moderate intensity of rainfall. This can be done by reseeding grasslands using *E. curvula* seeds. However, it is important to avoid overgrazing as this will modify competition between grasses and forbs to the advantage of the later functional groups, which may lead to less feed for animals. Increaser species are more adapted to low soil moisture than decreaser species. Increaser grass and forbs species are more drought tolerant than decreaser grass species. Therefore, increaser grass species will be more tolerant to predicted future rainfall reduction scenarios than decreaser grass species.

Chapter 4

Herbaceous structure, biomass production and rain use efficiency response to rainfall interception and resting period in the semi-arid grassland area of South Africa

4.1 Abstract

Reduction in rainfall is amongst the major climate change manifestation phenomena, and will have a significant impact on grassland ecosystems. A split plot experimental design was used to investigate the interactive effect of rainfall interception (rainfall reduction) and resting period (70 and 90 days) on herbaceous biomass production and rainwater use efficiency in semi-arid grasslands of South Africa. Different levels of rainfall interception were setup as main plot treatments, whereas resting periods were set as sub-plot treatments. Four 0.5 m × 0.5 m quadrats were harvested in spring, summer and autumn of 2016/17 and 2017/18 from each sub-plot to determine herbaceous species structure, aboveground biomass production and rainwater use efficiency (RUE). Grasses were most affected by rainfall interception than forbs at the 30% and 60% rainfall interception levels. In contrast, the forbs were more affected at 15% rainfall interception whereas the grasses showed resilience up to 15% interception in rainfall. The RUE was higher at 30% rainfall interception and 70-day resting period in almost all three seasons, except in spring 2016/17. Our results show that herbaceous above ground biomass showed resilience up to 15% interception but were affected more as the rainfall interception exceeded 30%. The predicted reduction in rainfall may result in domination of forbs and increase grass species in the grassland.

Keywords: forbs; grass; decrease; rainwater use efficiency

4.2 Introduction

Reduction in rainfall will have a significant impact on water resource availability in the grassland (Saadat *et al.* 2011; Mouatadid *et al.* 2018). One of the major challenges for ecologists today is assessing mechanisms that determine ecosystem response and recovery as well as ecological changes that come as a result of climatic changes and frequent extreme climate events (Smith 2011). However, the response of the rangelands to rainfall interception is highly variable and ranges from minimal level impacts (Kreyling *et al.* 2008; Jentsch *et al.* 2011; Dreesen *et al.* 2012) to prolonged change in ecosystem function structure and recovery (White *et al.* 2000; Haddad *et al.* 2002; Breshears *et al.* 2005; Ciais *et al.* 2005). Reduced rainfall and its extremes could alter the ecosystem function, depending on its influence on botanical composition and abundance of the species impacted (Hoover *et al.* 2014), and might even lead to soil erosion because of loss of vegetation cover.

Rainfall dictates to a large extent the availability of soil moisture and species abundance in arid and semi-arid ecosystems (Muldavin *et al.* 2008; Collins *et al.* 2008). Cutting of vegetation by grazing animals is a common occurrence in the grassland ecosystem (Zhang *et al.* 2018). The intensity of grazing and resting can impact the ability of certain species to compete and survive under reduced rainfall. Continuous grazing without resting could exacerbate the negative impacts of environmental stress on plant production (Bork *et al.* 2017).

Studies have shown that resistance strategies have been developed by certain plant species to maintain their reproductive capabilities and stability (Volaire 2018). Some plants have tolerance strategies to resist combinations of defoliation and environmental stress (Feller *et al.* 2014). Indigenous grass species are often the most dominant plants because of their superior adaptation to stress and extreme conditions such as water stress and extensive grazing, and thus preserve stability and productivity of the rangeland in semi-arid environments (Mischkolz *et al.* 2013).

The increase in abundance of unpalatable functional groups – such as some increaser grass species and forbs, at the expense of palatable and taller grass species, as a result of overgrazing and extreme weather events such as reduced rainfall is often used as an indication of degradation (Koerner & Collins 2014a). However, increases in these unpalatable functional groups may not be completely unnecessary to the functioning of the rangeland as they still provide soil cover (Siebert & Scogings 2015). For example, shrubs are high-quality food for

browsers in South African rangelands (Du Toit 2003). However, the response of forbs to common drivers of vegetation dynamics such as grazing and rainfall variability remains understudied (Siebert & Scogings 2015).

Therefore, it is important to know how grasslands respond to decreasing rainfall in the southern African region and how the extent of reduction in rainfall and grazing by animals and resting will affect the ecosystem species dynamics and biomass productivity of the system and state transitions. This can be done through monitoring the aboveground biomass yield, in particular by focusing on the dynamics of grass and forb composition and abundance under anticipated rainfall reduction climate scenarios and their response to resting and how the two interact to affect the ecosystem in South Africa (Báez *et al.* 2013). The objective of this study was to investigate the impact of simulated rainfall interception or deficit and resting periods on seasonal change in herbaceous species vegetation structure and aboveground biomass production of natural grassland in the semi-arid areas of South Africa.

4.3. Materials and methods

4.3.1. Site description

The study was conducted at Hatfield Experimental Farm, University of Pretoria, The farm is situated at an altitude of 1372 m above sea level. The coordinates of the study sites are 25°45' S and 28°16' E. The farm is situated in a summer rainfall area with a long-term mean annual rainfall of 674 mm (Talore 2015). The long-term mean cumulative monthly rainfall and the cumulative monthly rainfall during the study period are presented in Figure 4.1. Similarly, the long-term mean monthly temperature and mean monthly temperature during the study period are presented in Figure 4.2. The soil on the farm is categorized as non-calcareous with a homogenous red colour, weak structure of Hutton form and is sandy loam with 32.1 – 34.3% clay (Soil Classification Working Group 1991) and has a pH (H₂O) of 5.1 in a 2.5:1 soil–water ratio (Table 4.1). The research was conducted by using rainout shelters that was constructed in 2013 on a natural and unfertilized semi-arid grassland vegetation (Talore 2015, Mucina & Rutherford 2006) in a site excluded from grazing for more than 60 years. Initial changes in vegetation structure associated with the rainfall interception and resting periods for 2013/14 and 2013/14 were described by Talore (2015).

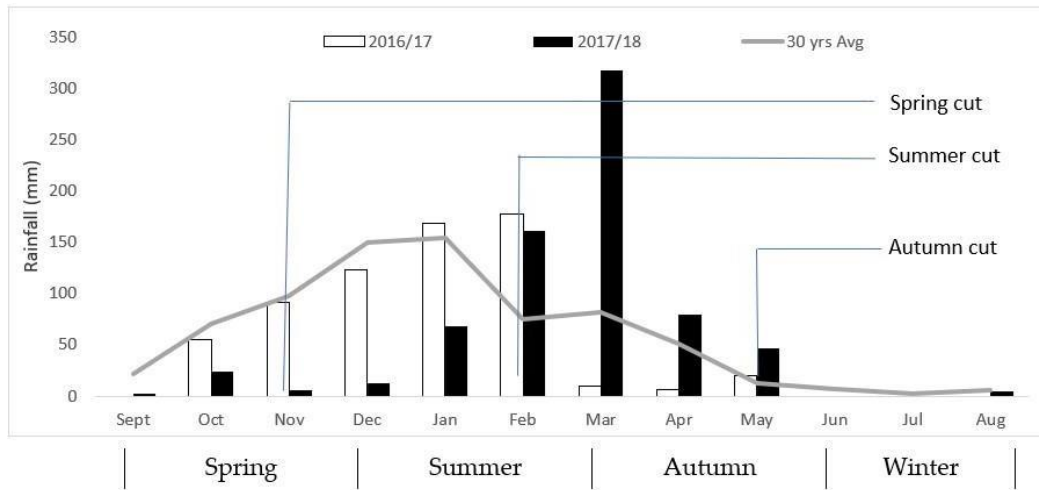


Figure 4.1 Thirty years average and monthly average rainfall (mm) for University of Pretoria Experimental Farm

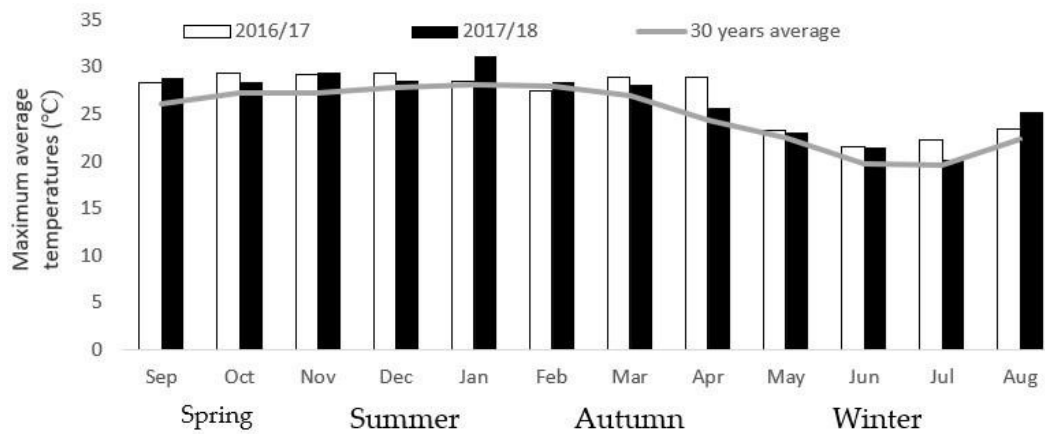


Figure 4.2 Thirty years average temperatures and three year monthly average temperatures (°C) for University of Pretoria Experimental Farm

Table 4.1 Soil pH, sand%, clay% and silt% at different rainfall interception and resting periods

Effects	pH	Sand %	Clay %	Silt %
RI ¹				
0%	5.1	53.1	32.1	14.9
15%	5.1	50.7	35.6	16.9
30%	5.1	48.7	33.8	17.5
60%	5.1	51.2	34.3	14.4
RP ²				
70 days	5.1	51.2	33.7	15.1
90 days	5.1	50.6	34.2	16.7

¹ RI: rainfall interception; ² RP: resting period

4.3.2. Rainout shelters and resting periods

Rainout shelters were established (Yahdjian & Sala 2002) with modification (Talore 2015). Rainfall interception was employed as main plot treatment at four levels of interception, namely 15%, 30%, 60% and 0% (control/ambient). The main plot treatments were each replicated five times in a split plot experimental design and two resting periods (75 and 90 days) were introduced as a sub-plot treatment. The main plots were 49 m² (7 m × 7 m and were covered by metal frame structures with V-shaped clear ultraviolet filter free acrylic bands on top. The bands were constructed with a longitudinal plate of 120° and a mean height of 1 m at the lowest side of the shelter was maintained. Each acrylic band was 7 m long and had a width of 12 cm. The 15% rainfall interception was achieved by laying nine acrylic bands parallel to each other with 68.5 cm space between bands. The 30% rainfall interception was achieved by laying 19 acrylic bands parallel to each other with 26.8 cm between bands, whereas 60% rainfall interception was achieved by laying 35 acrylic bands parallel to each other with 8.5 cm space between bands. Water was collected from the acrylic material and channelled through the gutters away from the plots. The experimental plots were sub-divided into two sub-plots (3.5 m × 7 m) to determine the effect of resting period (70 and 90 days). A 25-cm ditch was excavated along the boundary of the site to avoid water runoff into the plots. Ambient rainfall was measured after each rainfall event using five rain gauges that were scattered over the experimental site.

4.3.3. Data collection

Plant height and tuft diameter within each quadrat were measured with a tape measure. The grasses and forbs were measured separately. To have a similar starting point, all grasses and forbs in all pots were cut at a height of 5 cm above the ground at the beginning of the research trial in September 2016 and 2017. The sub-plot treatments were harvested to determine aboveground biomass production in spring, summer and autumn of 2016/17 and 2017/18. Four 0.5 m × 0.5 m (0.25 m²) quadrats of herbage were harvested from each sub-plot. Herbaceous vegetation was separated into functional groups (grasses and forbs) as shown in Table 4.2. Grasses were further categorized into their ecological statuses (increasers or decreaseers). The harvested herbage samples were oven dried at 60 °C for 72 hours to a constant weight [AOAC 2002]. Rainwater use efficiency (RUE) was calculated as the amount of herbaceous aboveground dry matter produced per millimetre of rainwater received between two consecutive harvests by the plots (Talore 2015). Long-term rainfall and temperature data were acquired from Hatfield Experimental Farm Station (Station number 0513465-1) weather records kept by South African Weather Services.

Table 4.2 Plant species occurring at the experimental site

Species	Functional Group	Ecological Status
<i>Eragrostis curvula</i>	Grass	Increaser II
<i>Cynodon dactylon</i>	Grass	Increaser II
<i>Digitaria eriantha</i>	Grass	Decreaser
<i>Setaria nigrirostris</i>	Grass	Decreaser
<i>Themeda triandra</i>	Grass	Decreaser
<i>Heteropogon contortus</i>	Grass	Increaser II
<i>Setaria sphacelata</i>	Grass	Decreaser
<i>Eragrostis barbinodes</i>	Grass	Increaser II
<i>Melinis repens</i>	Grass	Increaser II
<i>Brachiaria serrata</i>	Grass	Decreaser
<i>Aristida congesta</i>	Grass	Increaser II
<i>Ipomoea crassipes</i>	Forb	Invader
<i>Rhyncosia monophylla</i>	Forb	Invader
<i>Verbena tenuisecta</i>	Forb	Invader
<i>Vermonia oligocephala</i>	Forb	Invader

4.3.4. Statistical analysis

The plots were arranged in a split plot design with rainfall interception being the main plot treatment, whereas resting period was the sub-plot treatment. Data for the three seasons for each year were analysed separately because of the observed significant ($P < 0.05$) three-way interaction effect between rainfall interception, resting period and season during the preliminary analysis of the data. Data on biomass yield, sward height and rain use efficiency were analysed with two-way analysis of variance (ANOVA) using the general linear model procedure (Proc GLM) (SAS 2008). The factors that were tested were rainfall interception, resting periods and their interactions on biomass yield, sward height and RUE. The data were tested for normality before they were analysed. Where the data were not normally distributed (Shapiro-Wilk test < 0.9), they were transformed with square root or log function to normalize them. Where transformed data were used for analysis, the original mean values were retained in the table, but the mean separation was reported using the transformed data. Where the factors showed significant effect on the parameters, least square means (LSM) were separated using Tukey's test at a significance level of 5%. The results are presented in tabular form, where there was no interaction between rainfall interception and resting period. However, where there were significant interaction effects, the results are presented in a figure.

4.4. Results

Data were presented by season (spring, summer and autumn). The parameters included sward height, overall biomass yield, herbaceous structure, ecological status of the grass species (decreasers and increasers) and rainwater use efficiency over two years (2016/17 and 2017/18).

4.4.1. Seasonal vegetation sward height response to rainfall interception and resting period

Spring Cut

There was a significant ($P < 0.05$) interaction effect between rainfall interception and resting period on vegetation sward height in 2016/17 (Figure 4.3), but not in 2017/18 (Table 4.3). Regardless of the rainfall interception level, resting for 90 days resulted in a significantly ($P < 0.05$) taller sward height than the 70-day resting period in 2017/18 (Table 4.3). On the other hand, compared with control (ambient rainfall), the 60% rainfall interception treatment significantly ($P < 0.05$) reduced the sward height in 2017/18 (Table 4.3) whereas similar effect was observed in 2016/17 only for plots subjected to 90-day resting period (Figure 4.3). In contrast, in 2016/17 season the effect of rainfall interception was not significant when the plots were harvested after 70-day resting period. Similarly, 90 days resting resulted in a higher plant height when the rainfall interception was set at 0%, 15% and 30%, whereas at 60% rainfall interception resting period had no effect ($P < 0.05$).

Summer Cut

Rainfall interception and resting period had no significant ($P < 0.05$) interaction effect on the vegetation sward height in the two years (Table 4.3). Rainfall interception at 60% significantly ($P < 0.05$) reduced sward height in both years, whereas the effect of resting period was inconsistent over the years. During the summer of 2016/17, resting periods of 70 days led to a significant increase in sward height compared with 90 days. This was in contrast to the summer season of 2017/18, which did not show any significant ($P < 0.05$) sword height difference between resting periods.

Autumn Cut

In both years, there was no significant interaction effect between rainfall interception and resting period on the sward height. Generally, rainfall interception and resting period had a significant effect on vegetation sward height in both years. Unlike the spring cut, in the autumn cut, resting for 70 days resulted in a significantly taller sward height than the 90-day resting period in 2016/17 and 2017/18 growing seasons. Meanwhile, compared with the ambient rainfall, 60% rainfall interception treatment significantly ($P < 0.05$) reduced the sward height in

2016/17, but not in 2017/18 growing seasons (Table 4.3).

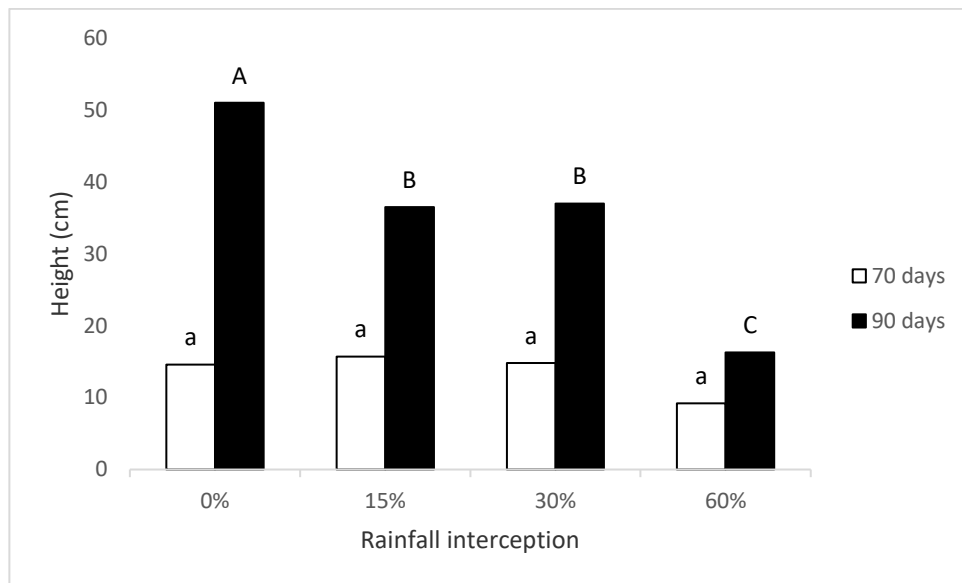


Figure 4.3 Interaction effect of rainfall interception and resting period on vegetation sward height in spring 2016/17. Different superscripts in the same cutting interval show significant difference.

Table 4.3. Main effect of resting period and rainfall interception on vegetation sward (mean $\pm$ S.E) height (cm)

Main effects	2017/18				
	Summer	Autumn	Spring	Summer	Autumn
Rainfall interception					
0%	45.0 $\pm$ 3.16 ^a	15.7 $\pm$ 0.88 ^a	16.2 $\pm$ 1.01 ^a	20.4 $\pm$ 1.18 ^a	16.8 $\pm$ 1.05 ^{ab}
15%	42.8 $\pm$ 3.16 ^a	16.2 $\pm$ 0.88 ^a	15.8 $\pm$ 1.01 ^a	19.9 $\pm$ 1.18 ^a	17.5 $\pm$ 1.05 ^{ab}
30%	38.9 $\pm$ 3.16 ^a	16.7 $\pm$ 0.88 ^a	15.9 $\pm$ 1.01 ^a	21.7 $\pm$ 1.18 ^a	19.7 $\pm$ 1.05 ^a
60%	28.4 $\pm$ 3.16 ^b	10.4 $\pm$ 0.88 ^b	9.8 $\pm$ 1.01 ^b	13.1 $\pm$ 1.18 ^b	15.6 $\pm$ 1.05 ^b
<i>P</i> -value	0.013	0.001	0.002	0.001	0.164
Resting period					
70 days	41.5 $\pm$ 1.69 ^a	18.0 $\pm$ 0.51 ^a	13.6 $\pm$ 0.48 ^b	19.6 $\pm$ 0.67 ^a	19.2 $\pm$ 0.79 ^a
90 days	36.1 $\pm$ 1.69 ^b	11.5 $\pm$ 0.51 ^b	15.3 $\pm$ 0.48 ^a	18.0 $\pm$ 0.67 ^a	15.3 $\pm$ 0.79 ^b
<i>P</i> -Value	0.040	<0.001	0.021	0.107	0.003

Different small letter superscripts along the same column in the same year and season were significantly different ($p < 0.05$); S.E: standard error

4.4.2. Seasonal biomass production response of different functional groups and grass ecological status to rainfall interception and resting period

In both years, there were no significant interaction effect between rainfall interception and resting period on both grasses and forbs biomass production (Tables 4.4, 4.5). Regardless of the growing season, resting for 90 days resulted in a significantly ($P < 0.05$) higher forbs biomass production than 70-day resting period. On the other hand, 15% rainfall interception resulted in a significantly ($P < 0.05$) lower forbs biomass production than the ambient rainfall in both years. Similar to forbs, resting for 90 days resulted in a significantly ($P < 0.05$) higher grass biomass production than 70 days resting (Table 4.5). Compared with the ambient rainfall, 60% rainfall interception severely reduced grass biomass production in both years.

Table 4.4. Main effect of resting period and rainfall interception on forbs (mean $\pm$ S.E) aboveground biomass yield ($\text{kg}\cdot\text{ha}^{-1}$)

Main Effects	2016/17			2017/18		
	Spring *	Summer ⁺	Autumn ⁺	Spring	Summer ⁺	Autumn ⁺
Rainfall interception						
0%	364 $\pm$ 285.2 ^a	618 $\pm$ 149.5 ^a	113 $\pm$ 52.9 ^b	519 $\pm$ 105.6 ^a	411 $\pm$ 105.7	107 $\pm$ 42.6 ^b
15%	68 $\pm$ 312.4 ^b	140 $\pm$ 158.6 ^b	123 $\pm$ 52.9 ^b	265 $\pm$ 112.0 ^b	243 $\pm$ 100.3	111 $\pm$ 61.5 ^b
30%	678 $\pm$ 238.6 ^a	513 $\pm$ 149.5 ^a	220 $\pm$ 52.9 ^{ab}	328 $\pm$ 112.0 ^{ab}	204 $\pm$ 125.1	137 $\pm$ 45.2 ^a
60%	536 $\pm$ 208.3 ^a	448 $\pm$ 149.5 ^a	349 $\pm$ 56.1 ^a	290 $\pm$ 105.6 ^{ab}	338 $\pm$ 100.3	282 $\pm$ 45.2 ^a
<i>P</i> -value	0.470	0.534	0.016	0.341	0.550	0.039
Resting period						
70 days	104 $\pm$ 149.5 ^b	478 $\pm$ 105.7	293 $\pm$ 32.4 ^a	225 $\pm$ 74.6 ^b	266 $\pm$ 81.9	143 $\pm$ 36.1
90 days	719 $\pm$ 217.8 ^a	382 $\pm$ 109.0	110 $\pm$ 38.6 ^b	476 $\pm$ 79.2 ^a	332 $\pm$ 70.9	175 $\pm$ 33.4
<i>P</i> -value	0.033	0.178	0.002	0.028	0.552	0.626

Different small letter superscripts along the same column in the same season were significantly different ($p < 0.05$); (*): log transformed; (⁺): square root transformed; S.E: standard error

Table 4.5 Main effect of resting period and rainfall interception on grass (mean $\pm$ S.E) aboveground biomass yield (kg.ha⁻¹)

Main Effects	2016/17		2017/18		
	Spring ⁺	Summer	Spring ⁺	Summer	Autumn
Rainfall interception					
0%	744 $\pm$ 82.0 ^a	2164 $\pm$ 254.3 ^a	659 $\pm$ 57.7 ^a	1257 $\pm$ 147.3 ^a	837 $\pm$ 102.7 ^{ab}
15%	624 $\pm$ 82.0 ^{ab}	2258 $\pm$ 254.3 ^a	719 $\pm$ 57.7 ^a	1124 $\pm$ 147.3 ^a	840 $\pm$ 102.7 ^{ab}
30%	459 $\pm$ 82.0 ^b	2064 $\pm$ 254.3 ^a	576 $\pm$ 57.7 ^a	1107 $\pm$ 147.3 ^a	1015 $\pm$ 102.7 ^a
60%	222 $\pm$ 82.0 ^c	679 $\pm$ 254.3 ^b	171 $\pm$ 57.7 ^b	346 $\pm$ 147.3 ^b	578 $\pm$ 102.7 ^b
<i>P</i> -value	<0.001	0.003	<0.001	<0.001	0.069
Resting period					
70 days	306 $\pm$ 58.4 ^b	1733 $\pm$ 120.7 ^a	402 $\pm$ 41.1 ^b	990 $\pm$ 100.2 ^a	998 $\pm$ 67.1 ^a
90 days	719 $\pm$ 58.4 ^a	1850 $\pm$ 120.7 ^a	661 $\pm$ 41.1 ^a	928 $\pm$ 100.2 ^a	636 $\pm$ 67.1 ^b
<i>P</i> -value	<0.001	0.501	<0.001	0.672	0.002

Different small letter superscripts along the same column in the same and season were significantly different ($P < 0.05$); (⁺): square root transformed; S.E: standard error

There was no significant ($P > 0.05$) interaction effect between rainfall interception and resting period on grass yield and ecological status. Resting for 90 days significantly ($p < 0.05$) increased the biomass production of both decreaser (Table 4.6) and increaser (Table 4.7) grass species in both years. In both years, the 60% rainfall interception treatments significantly ($P < 0.05$) reduced biomass production of decreasers (Table 4.6) and increaser (Table 4.7) grass species compared with 0% rainfall interception treatments. Moreover, resting period resulted in a significantly ($P < 0.05$) higher decreaser (Table 4.6) and increaser (Table 4.7) biomass yield at 90 days resting than 70 days in both years.

Table 4.6 Main effect of resting period and rainfall interception on decreaser grass (mean $\pm$ S.E) species ($\text{kg}\cdot\text{ha}^{-1}$)

Main Effects	2016/17			2017/18		
	Spring ⁺	Summer *	Autumn *	Spring	Summer	Autumn *
Rainfall interception						
0%	371 $\pm$ 55.3 ^a	1860 $\pm$ 512.1 ^a	370 $\pm$ 59.3 ^a	301 $\pm$ 45.8 ^a	632 $\pm$ 92.9 ^a	450 $\pm$ 91.7
15%	344 $\pm$ 49.5 ^{ab}	1068 $\pm$ 512.1 ^a	330 $\pm$ 59.3 ^a	250 $\pm$ 45.8 ^a	602 $\pm$ 103.9 ^a	394 $\pm$ 91.7
30%	203 $\pm$ 64.5 ^b	580 $\pm$ 512.1 ^{ab}	232 $\pm$ 62.9 ^a	151 $\pm$ 72.5 ^a	351 $\pm$ 103.9 ^{ab}	415 $\pm$ 91.7
60%	127 $\pm$ 55.3 ^c	243 $\pm$ 512.1 ^b	46 $\pm$ 62.9 ^b	107 $\pm$ 72.5 ^b	113 $\pm$ 103.9 ^b	218 $\pm$ 97.3
<i>P</i> -value	0.002	0.210	<0.001	0.032	0.011	0.369
Resting period						
70 days	138 $\pm$ 61.2 ^b	735 $\pm$ 321.2	323 $\pm$ 43.2 ^a	102.7 $\pm$ 43.5 ^b	418 $\pm$ 50.0	529 $\pm$ 66.9 ^a
90 days	385 $\pm$ 56.0 ^a	1141 $\pm$ 302.9	166 $\pm$ 43.2 ^b	256.5 $\pm$ 27.5 ^a	431 $\pm$ 42.6	209 $\pm$ 64.9 ^b
<i>P</i> -value	0.006	0.372	0.015	0.014	0.854	0.005

Different small letter superscripts along the same column in the same year and season were significantly different ($P < 0.05$); (*): log transformed; (+): square root transformed, S.E: standard error.

Table 4.7 Main effect of resting period and rainfall interception on increaser grass (mean $\pm$ S.E) species (kg.ha⁻¹)

Main Effects	2016/17			2017/18		
	Spring ⁺	Summer	Autumn	Spring	Summer	Autumn ⁺
Rainfall interception						
0%	413 $\pm$ 69.2 ^a	1251 $\pm$ 291.5 ^{ab}	566 $\pm$ 89.7 ^a	300.7 $\pm$ 45.8 ^a	631.5 $\pm$ 92.9 ^a	409 $\pm$ 98.6
15%	280 $\pm$ 69.2 ^a	1053 $\pm$ 260.7 ^{ab}	701 $\pm$ 89.7 ^a	250.3 $\pm$ 45.8 ^a	601.9 $\pm$ 103.9 ^a	448 $\pm$ 98.6
30%	309 $\pm$ 69.2 ^a	1484 $\pm$ 260.7 ^a	742 $\pm$ 89.7 ^a	150.7 $\pm$ 72.5 ^{ab}	351.3 $\pm$ 103.9 ^{ab}	646 $\pm$ 98.6
60%	134 $\pm$ 77.4 ^b	463 $\pm$ 260.7 ^b	299 $\pm$ 89.7 ^b	116.6 $\pm$ 72.5 ^b	113.1 $\pm$ 103.9 ^b	295 $\pm$ 104.6
<i>P</i> -value	0.115	0.087	0.001	0.032	0.011	0.222
Resting period						
70 days	193 $\pm$ 43.3 ^b	1026 $\pm$ 144.8	792 $\pm$ 63.5 ^a	102.7 $\pm$ 43.5 ^b	418.3 $\pm$ 50.0	514 $\pm$ 71.9 ^a
90 days	375 $\pm$ 46.0 ^a	1099 $\pm$ 136.5	362 $\pm$ 63.5 ^b	256.5 $\pm$ 27.5 ^a	430.6 $\pm$ 42.6	384 $\pm$ 69.8 ^b
<i>P</i> -value	0.011	0.722	<0.001	0.014	0.854	0.194

Different small letter superscripts along the same column in the same year and season were significantly different ($P < 0.05$); (⁺): square root transformed.

Summer Cut

There was no significant interaction ($P > 0.05$) effect between rainfall interception and resting period on forbs and grass biomass yield. Resting period had no significant ($P > 0.05$) effect on forbs biomass production in either year (Table 4.4). However, in 2016 /17, the 15% rainfall interception resulted in a significantly ($p < 0.05$) low forbs biomass production. In contrast, in 2017/18, rainfall interception had no significant effect on forbs biomass production. Similarly to forbs, resting period had no significant ($P > 0.05$) effect on grass biomass production in both years. However, the 60% rainfall interception severely decreased grass biomass production compared with the rest of the rainfall interception treatments. Rainfall interception and resting period had no significant ($P > 0.05$) interaction effect on grass ecological status in either year. In both years, resting period had no significant ($P > 0.05$) effect on biomass production of both decreaser (Table 4.6) and increaser (Table 4.7) grass species. The decreaser species grass biomass production at 60% rainfall interception was 87% less than 0% rainfall interception in 2016/17 whereas it was 82% less than 0% rainfall interception in 2017/18. Compared to 0% interception, the increaser grass species biomass production of the 60% rainfall interception was reduced by 63% in 2016/17 and by 82% in 2017/18.

Autumn Cut

Rainfall interception and resting period had no significant interaction effect on forbs in both years (Table 4.4). However, there was a significant ($P < 0.05$) interaction effect between resting period and rainfall interception on forbs biomass production in 2016/17 (Figure 4.4), but not in 2017 /18 (Table 4.5). Unlike the spring and summer seasons, 60% rainfall interception in autumn resulted in a significantly ($P < 0.05$) high forb biomass production in 2016/17 compared with 0% and 15% rainfall interception whereas both 30% and 60% rainfall interceptions had a significantly high forbs biomass production in 2017/18 growing season compared with 0% and 15% rainfall interception. The 70-day resting period resulted in a more significant ($P < 0.05$) high forbs biomass production than 90 days. Similarly, the 70-day resting period had the higher grass biomass production than 90 days resting period in both years. In 2017/18, rainfall interception at 30% resulted in a significantly higher grass biomass production compared with the 60% rainfall interception treatments.

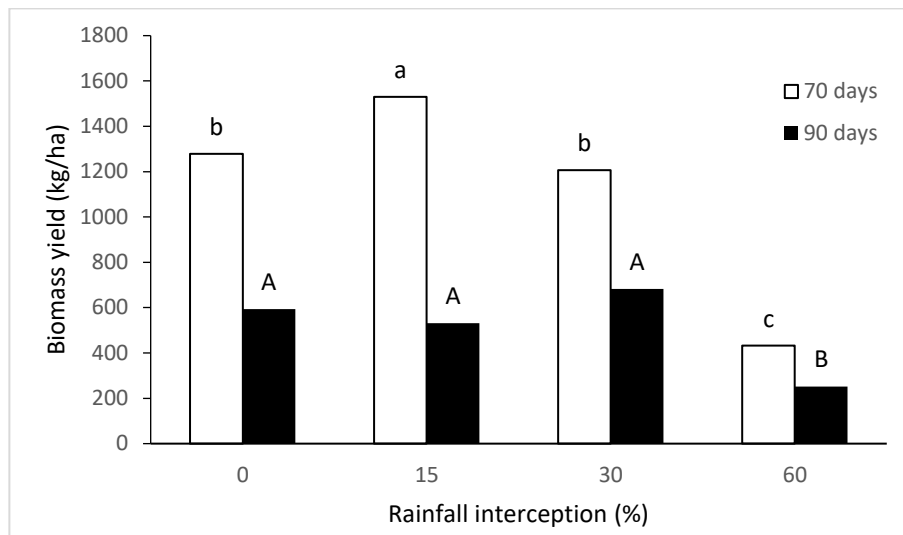


Figure 4.4 Mean interaction effect of rainfall interception and resting period on grass biomass yield in autumn 2016/17. Different superscripts at different cutting intervals are significantly different

During the 2016/17 season there was a significant ($P < 0.05$) interaction effect on grass biomass yield between rainfall interception and resting period. The 60% rainfall interception significantly reduced grass biomass production compared with the rest of the treatments. Resting the veld for 70 days gave more biomass production in the 0%, 15% and 30% treatments, but not in the 60% rainfall interception plots. Compared with the 90-day resting period, resting for 70 days resulted in a significantly ($P < 0.05$) high decreaser (Table 4.6) and increaser (Table 4.7) grass biomass yield in both years. At 60% rainfall interception, the decreaser grass species biomass production was reduced by 89% compared with ambient treatment in 2016/17. Although the increaser grass biomass production at 60% rainfall interception was significantly ($P < 0.05$) lower than 15% and 30% rainfall interception biomass production, it was not significantly different to 0% rainfall interception in 2016/17.

4.4.3. Seasonal response in total aboveground biomass yield to rainfall interception and resting period

Spring Cut

There was no significant ($P > 0.05$) interaction effect between rainfall interception and resting period on total aboveground biomass yield in both years (Figure 4.5a, b). Resting for 90 days resulted in a significantly ($P < 0.05$) higher overall biomass yield in 2016/17 than the 70-day resting period. In 2017/18, 60% rainfall interception significantly ($P < 0.05$) reduced overall biomass yield compared with the rest of the rainfall interception treatments. Intercepting rainfall by 60% resulted in a 75% interception in overall biomass production in 2016/17, whereas it was reduced by 61% in 2017/18.

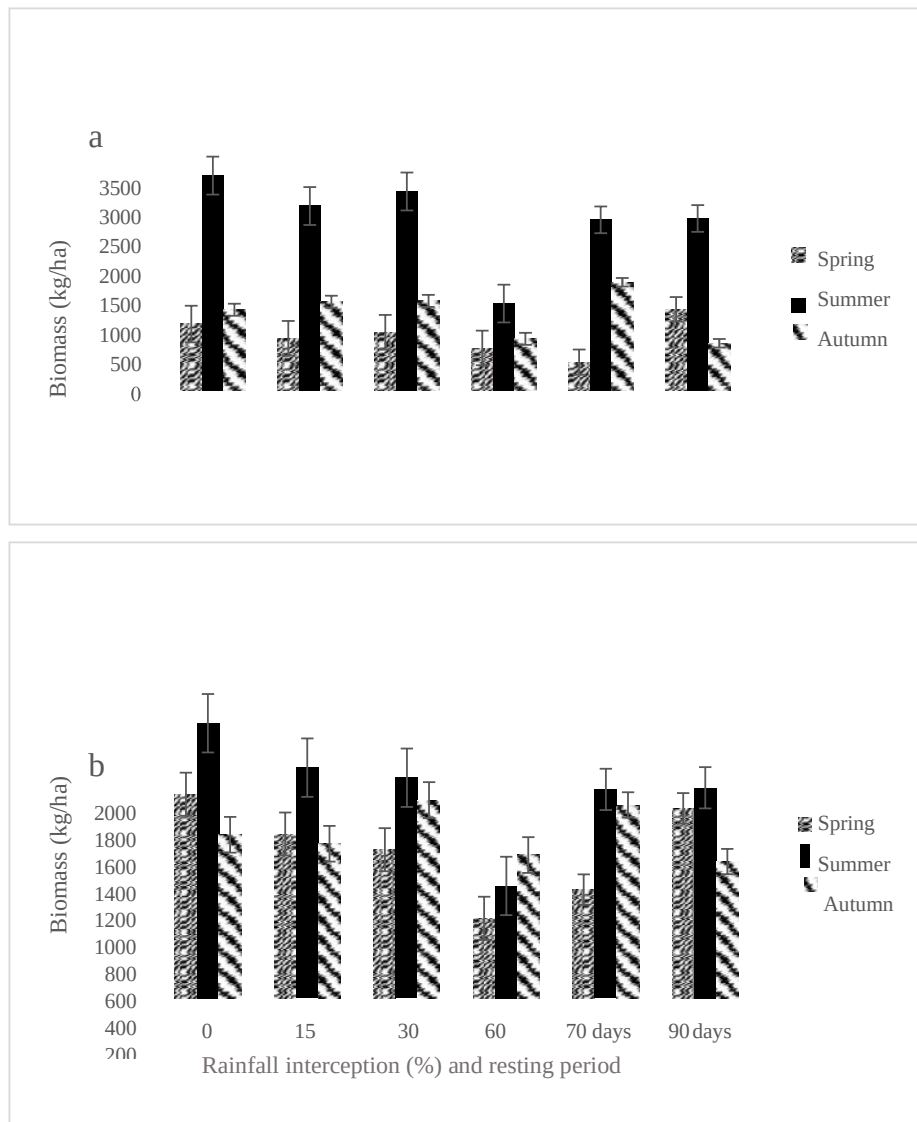


Figure 4.5 Interaction effect of resting period and rainfall interception on overall aboveground biomass yield (kg. ha^{-1}) in **(a)** 2016/17 and **(b)** 2017/18 (bars indicate standard error values)

Summer Cut

There was no significant ($P > 0.05$) interaction effect between rainfall interception and resting period on the total aboveground biomass yield in both years. In both years, 60% rainfall interception significantly ($P < 0.05$) reduced overall biomass yield compared with the rest of the rainfall interception treatments (Figure 4.5a,b). Intercepting rainfall by 60% resulted in 59% reduction in overall biomass production in both years compared with 0% rainfall interception.

Autumn Cut

Rainfall interception and resting period interaction had no significant ($P > 0.05$) effect on the total aboveground biomass yield in both years. In both years, resting for 90 days significantly decreased ($P < 0.05$) the overall biomass yield compared with the 70-day resting period. Rainfall interception had a significant effect on aboveground biomass ($P < 0.05$) at 60% rainfall interception in 2016/17 whereas it had no significant effect in 2017/18 in the same season.

4.4.4. Seasonal response in rainwater use efficiency to rainfall interception and resting period

Spring Cut

Rainfall interception and resting period interaction had a significant ($P < 0.05$) effect on rainwater use efficiency in both years (Figure 4.6a, b). In 2016 /17, the 90-day resting period resulted in a significantly high RUE compared with the 70-day resting period, irrespective of the rainfall interception. In both 2016/17 and 2017/18, RUE was significantly lower at 60% rainfall interception for the 70-day resting period, whereas for the 90-day resting period rainwater use efficiency was lowest, at 30% rainfall interception in 2016/17 and at 15% rainfall interception in 2017/18.

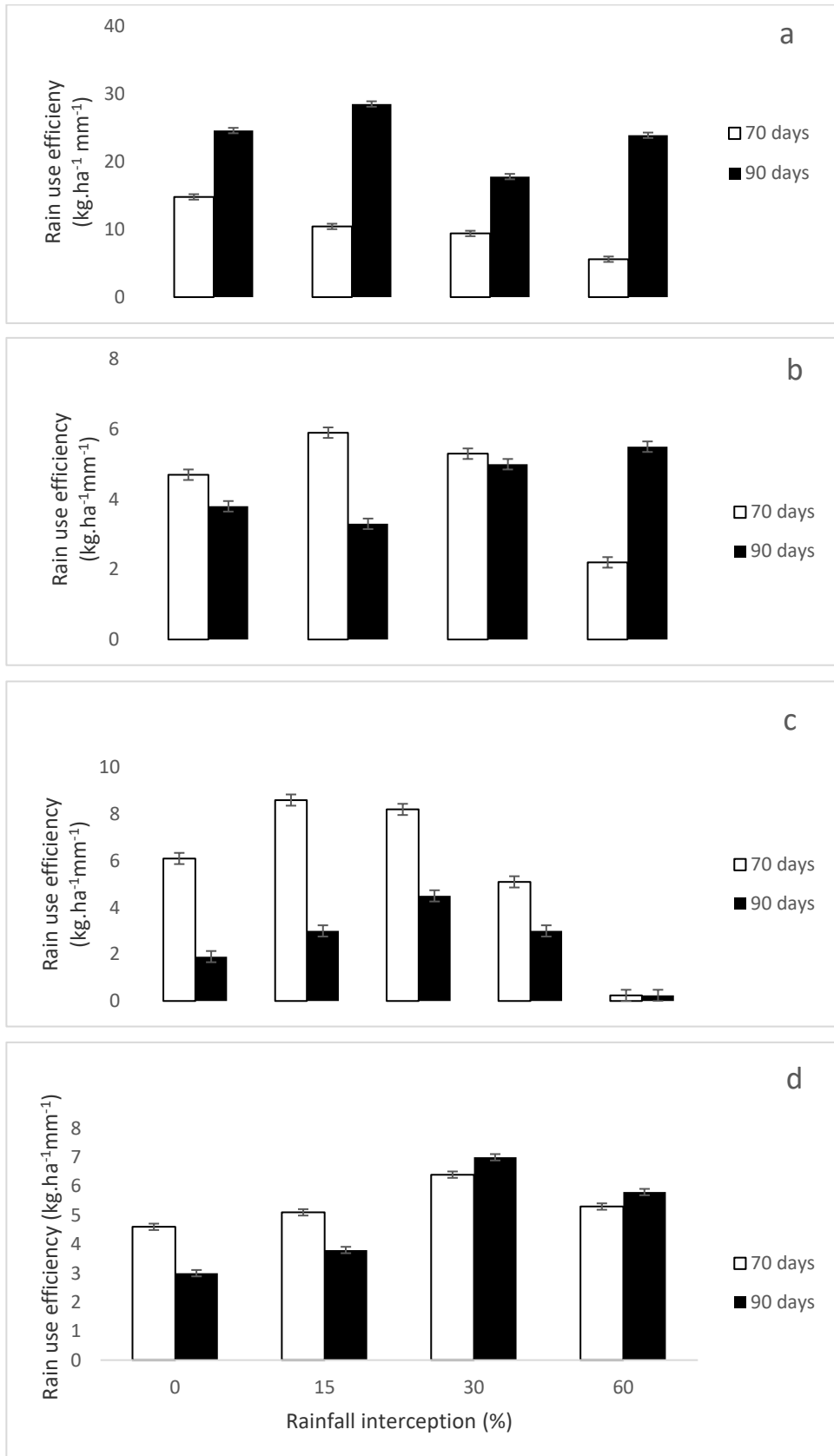


Figure 4.6 Interaction effects of rainfall interception and resting period on rainwater use efficiency in (a) spring 2016/17, (b) spring 2017/18, (c) autumn 2016/17 and (d) autumn 2017/18 Rain use efficiency (kg.ha⁻¹.mm⁻¹)

Bars indicate standard error values.

Summer Cut

There was no significant interaction effect between rainfall interception and resting period on RUE in both years. Rainfall interception and resting period had a significant ($P < 0.05$) effect on rain use efficiency in both years (Table 4.8). Resting for 70 days resulted in a significantly ($P < 0.05$) higher RUE than the 90-day resting period in both years. In both 2016/17 and 2017/18, the RUE was significantly ($P < 0.05$) reduced at 60% compared with the control as well as 15% and 30% rain interception treatments.

Table 4.8 Main effect of resting period and rainfall interception on rainwater use efficiency (mean $\pm$ S.E) ($\text{kg} \cdot \text{ha}^{-1} \cdot \text{mm}^{-1}$)

Main Effects	2016/17	2017/18
	Summer	Summer
Rainfall interception		
0%	12.6 ± 0.22^a	3.7 ± 0.17^a
15%	11.9 ± 0.22^b	4.1 ± 0.17^a
30%	13.2 ± 0.22^a	4.0 ± 0.17^a
60%	7.3 ± 0.22^c	1.9 ± 0.17^b
<i>p</i> -value	<0.001	<0.0001
Resting period		
70 days	12.5 ± 0.19^a	3.8 ± 0.11^a
90 days	9.9 ± 0.19^b	3.0 ± 0.11^b
<i>p</i> -value	<0.001	<0.001

Different small letter superscripts along the same column in the same year and season were significantly different ($P < 0.05$); S.E: standard error

Autumn Cut

Rainfall interception and resting period interaction had a significant ($p < 0.05$) effect on rainwater use efficiency in both years (Figure 4.6c, d). In 2016 /17, the 70-day resting period had significantly higher RUE than 90-day resting period across all the rainfall interceptions. In the 2016/17 season, the 60% rainfall interception had a significantly lower RUE compared with 0% rainfall interception at 70-day resting period, whereas there was no significant difference between 0% and 60% rainfall interception at 90-day resting period.

4.4.5. Overall relationship between rainfall interception, resting period and vegetation response parameters

Principal component analysis (PCA) was performed to investigate the overall

relationship between vegetation response parameters and rainfall interception and resting period. The first two PCAS accounted for 93% of the variation. The first PC correlated with *D. eriantha*, decreasers, *E. curvula*, and increasers in both years (Figures 4.7 and 4.8). *Digitaria eriantha* is a decreaser grass species that contributed most towards decreaser grass biomass production, whereas *E. curvula* had a greater contribution towards the increaser biomass in both years. On the other hand, forbs were correlated with PCA2, though not separated into species. *Ipomoea crisspes* was the most dominant forb in both years. At a lower rainfall interception (0% and 15% rainfall interception), *E. curvula* correlated well with the 70-day resting period (v1: 0% RI, 70 RP and v3: 15% RI, 70 RP), whereas *D. eriantha* correlated well with 90-day resting period (v2: 0% RI, 90 RP and v4: 15% RI, 90 RP) in 2016/17 (Figure 4.7). Similarly, forbs biomass production correlated well with an interception in rainfall (30% and 60% rainfall interception) at both 70- and 90-day resting periods in 2016/17 (Figure 17). Unlike the 2016/17 season, *D. eriantha* correlated well with the 70-day resting period for higher rainfall (0% and 15% interception) whereas forbs correlated well with lower rainfall (30% and 60% rainfall interception) treatments (Figure 4.8).

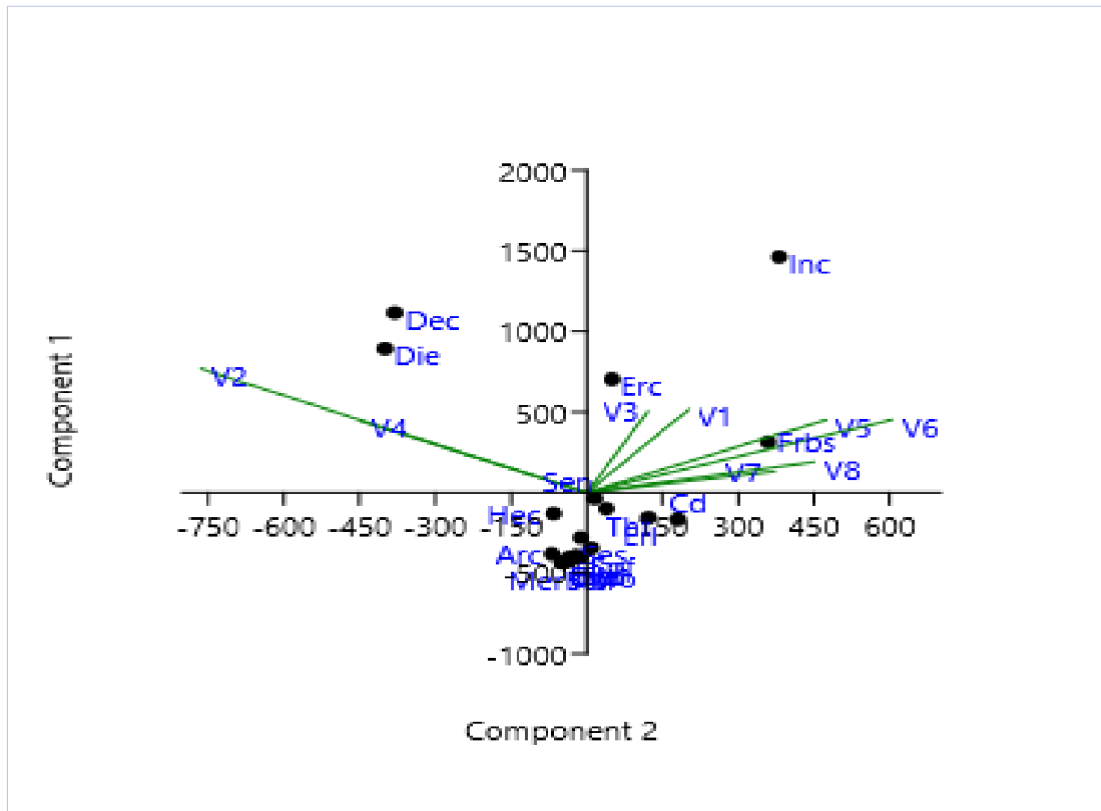


Figure 4.7 Principal component analysis plot showing the effect of resting period and rainfall interception on overall biomass yield ($\text{kg}\cdot\text{ha}^{-1}$) and other vegetation parameters in 2016/17

Key to symbols: black dots (•) indicate treatment and the season and vectors (—) indicate the direction of the relationship between vegetation parameters and treatments. The longer the vector radiating from the centre, the stronger the effects of the resting period and the resting period and the closer the dot to the vector the stronger the relationship between species and soil property

V1 = 0% RI, 70 RP, V2 = 0% RI, 90 RP, V3 = 15% RI, 70 RP, V4 = 15% RI, 90 RP, V5 = 30% RI, 70 RP, V6 = 30% RI, 90 RP, V7 = 60% RI, 70 RP, V8 = 60% RI, 90 RP. Cd: *Cynodon dactylon*, Die: *Digitaria eriantha*, Erc: *Eragrostis curvula*, Tht: *Themeda triandra*, Erl: *Eragrostis lehmaniana*, Spf: *Sporobolus fimbriatus*, Hec: *Heteropogon contortus*, Sen: *Setaria nigrirostris*, Ses: *Setaria sphacelata*, Cye: *Cymbopogon excavatus*, Umos: *Urochloa mosambicensis*, Erb: *Eragrostis barbinodes*, Arc: *Aristida congesta*, Erpl: *Eragrostis plana*, Brs: *Brachiaria serata*, Hyh: *Hyparrhenia hirta*, Mer: *Melinis repens*, Frbs: forbs, Dec: decreasers, Inc: increasers

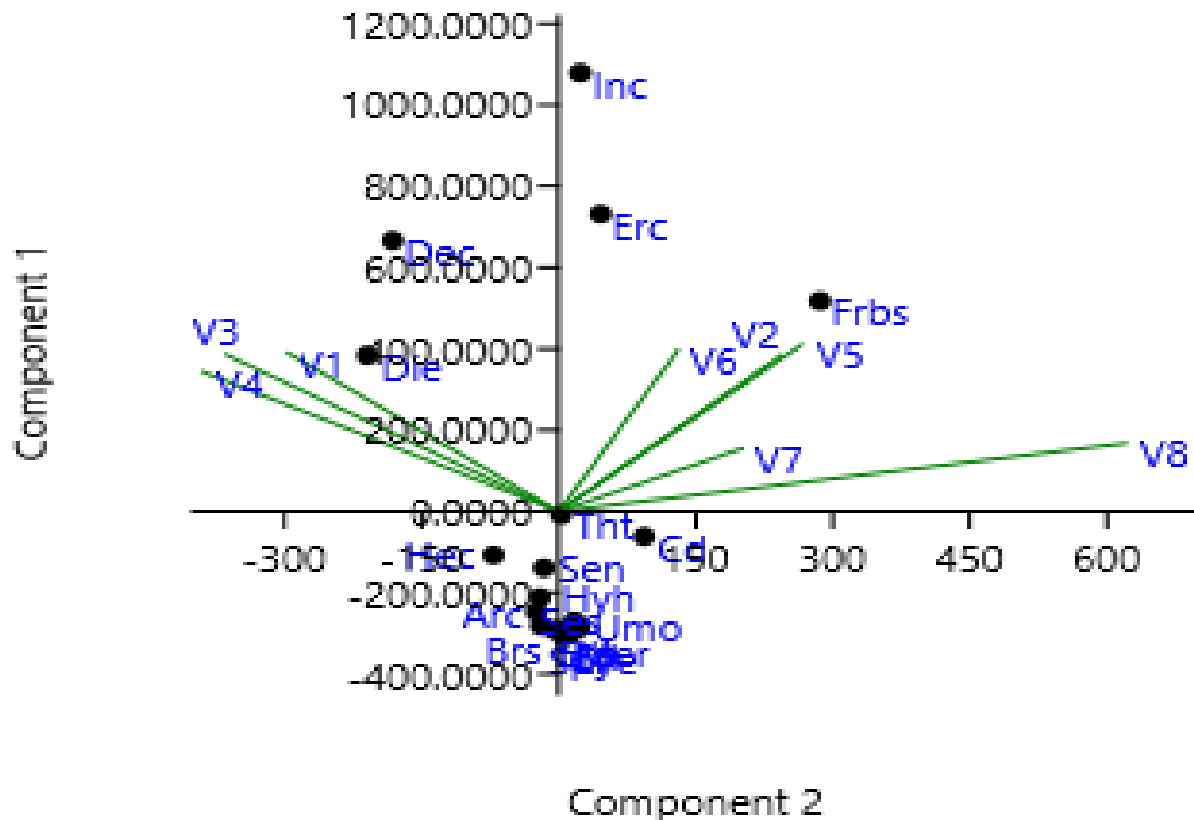


Figure 4.8 Principal component analysis plot showing the effect of resting period and rainfall interception on overall biomass yield ($\text{kg}\cdot\text{ha}^{-1}$) and other vegetation parameters in 2017/18

Key to symbols: black dots (•) indicate treatment and the season and vectors () indicate the direction of the relationship between vegetation parameters and treatments. The longer the vector radiating from the centre, the stronger the effects of the resting period and the closer the dot to the vector, the stronger the relationship between species and soil property

V1 = 0% RI, 70 RP, V2 = 0% RI, 90 RP, V3 = 15% RI, 70 RP, V4 = 15% RI, 90 RP, V5 = 30% RI, 70 RP, V6 = 30% RI, 90 RP, V7 = 60% RI, 70 RP, V8 = 60% RI, 90 RP. Cd: *Cynodon dactylon*, Die: *Digitaria eriantha*, Erc: *Eragrostis curvula*, Tht: *Themeda triandra*, Erl: *Eragrostis lehmaniana*, Spf: *Sporobolus fimbriatus*, Hec: *Heteropogon contortus*, Sen: *Setaria nigrirostris*, Ses: *Setaria sphacelata*, Cye: *Cymbopogon excavatus*, Umos: *Urochloa mosambicensis*, Erb: *Eragrostis barbinodes*, Arc: *Aristida congesta*, Erpl: *Eragrostis plana*, Brs: *Brachiaria serata*, Hyh: *Hypperhenia hirta*, Mer: *Melinis repens*, Hei: height, Ob: overall biomass, , Frbs: forbs, Dec: decreasers, Inc: increasers, RUE: rain use efficiency

4.5. Discussion

The current results showed that the vegetation height coincides with the vegetation biomass yield, which suggests that there is a positive relationship between vegetation height and the biomass production. The vegetation was taller at lower rainfall interception treatments (0% and 15%) than the higher rainfall interception treatments (30% and 60%). The heights were also affected by the seasons as the season with higher rainfall had taller vegetation (Table 4.3). Vegetation height and biomass are very much influenced by available resources such as nutrients and water (Derner *et al.* 2011). These results concur with those of (Snyman 2005a; Snyman 2009), who reported that vegetation growth mainly depends upon summer rainfalls, as the rainfall is generally lower in other seasons because of skewed distribution, particularly in summer rainfall areas.

Moreover, resting period affected vegetation height in different ways in different seasons. In spring, the vegetation was taller at the 90-day resting period rather than the 70 days one, whereas the opposite was true in autumn in both years. This is because in spring the extra 20 days for the 90-day resting period gave this resting period extra time to grow. On the other hand, the 70-day resting period had a taller vegetation than the 90-day resting period in autumn in both years. This could be because the 70-day resting period received rainfall just after it was cut and it was cut whereas getting summer rainfall and before the 90-day resting period was cut in summer. This gave an advantage to the 70-day resting period because the rainfall starts to decline in autumn and some annual plants begin to die. Height also correlated well with biomass in both years. Resting for 90 days in spring improved grass biomass production, whereas resting for 70 days improved grass biomass yield in autumn in both years. The higher biomass yield in the 70-day resting period in autumn is attributed to the 20-day delay for 90 days cutting in December as the rainfalls are beginning to decrease, whereas the 70-day resting period gets the summer rainfall (Figure 4.1).

Grass harvest sampling every 70 days and 90 days over two seasons in 2016/17 and three seasons in 2017/18 was able to show seasonal differences in terms of biomass production. This was also reported by (Snyman 2009; Ingram 2002). In this study, shorter resting periods improved grass biomass production in autumn whereas in spring longer resting periods improved grass biomass production. The 0%, 15% and 30% rainfall interception treatments had higher grass biomass production than the 60% rainfall interception. According

to Carlyle *et al.* (2014), the dominant grasses such as *D. eriantha* and *E. curvula* at various treatments appear to contribute more biomass production than the less dominant grass species such as *A. conaesta* and *M. repens*. Hence these grasses will determine whether the rangeland will be productive for animal production.

Rainfall interception significantly reduced overall biomass production only at 60% rainfall interception. This showed that the grasslands were able to show resilience by making adjustments in terms of species composition up to the level of 30% interception in rainfall. However, severe interception in rainfall amount (60%) would have a significantly negative impact on rangeland productivity, which would lead to lower biomass production and subsequently fodder for animal production (Figure 4.5). This means that in 2016/17 the rainfall was better. Hence it was possible to improve resilience of the system or support better growth by modifying the resting period (changing from 75 to 90 days), but such benefit would not be sustained with modification of resting period once the rainfall interception becomes severe.

The native herbage biomass production was not affected by up to 30% interception in rainfall owing to resilience of increaser species such as *E. curvula* that dominated the 15% and 30% rainfall interception plots (Figures 4.7 and 4.8). Del-Val & Crawley (2005) found that increasers were more tolerant to grazing than decreasers. In that study, three increaser grass species had a higher compensation regrowth after four episodes of clipping. As observed in the current study, *E. curvula* is able to regrow after it has been harvested, even at high frequencies.

There is an expectation that a reduction in rainfall associated with climate change will have a negative impact on natural grazing land in arid and semi-arid areas of sub-Saharan Africa (Hoffman & Vogel 2008). This is because forage production in these areas is sensitive to rainfall reduction, as in the current study site. This concurs with the results of Boone *et al.* (2017), who reported that the rangeland in sub-Saharan Africa is sensitive to climate change. In general, as expected, season had an impact on overall biomass production because summer had a higher biomass production than spring and autumn in both years. Here, higher temperature and rainfall is the main driving force for the higher biomass production recorded in summer than in spring and autumn. This agrees with studies that reported similar results pertaining the response of grassland biomass production to simulated climate change

(Breshears *et al.* 2005; Carlyle *et al.* 2014; Yahdjian & Sala 2006). The cumulative biomass yield was significantly higher in 2016/17 than in 2017/18 because of the higher rainfall amount received in 2016/17. This means that with the expected decrease in rainfall associated with climate change and subsequently decrease in biomass accumulation, farmers need to consider supplementing the animals and destocking where possible in the event of severe rainfall reduction encounters.

Decreasers are resilient up to 15% interception in rainfall thereafter. However, they are more prone to rainfall interception than the increaser grass species as they were dominant and performed much better at 0% and 15% rainfall interception plots whereas increasers were better performers at 30% and relatively even at 60% rainfall interceptions (Tables 4.6 and 4.7). This implies that continued rainfall reduction will potentially lead to disappearance of decreaser grass species such as *D. eriantha* and *T. triandra* in favour of increaser grass species such as *E. curvula* and *C. dactylon* and possibly forbs. In this study, the increaser grass species were more resilient to severe interception in rainfall (as judged from increase in rainfall interception) than decreaser grass species. The results from this study concur with the findings reported by (Snyman and Van Rensburg 1990), who reported that decreaser grass species fluctuate with variation in soil moisture whereas the increaser grass species were more resilient to water deficiency than decreaser grass species. This means that decreasers require more water to produce the same unit of biomass than increaser grass species or forbs that require less water. However, (Stampfli & Zeiter 2004) reported that vegetation changes induced by drought may shift vegetation from grass-dominated to forb dominated community.

This is in agreement with the finding of this study where grasses had a higher biomass production at 0%, 15% and 30% rainfall interception whereas forbs had higher biomass production at 60% rainfall interception and dominated the 30% and 60% rain interception plots. This could be partly related to the failure of grasses to produce seeds and grasses having shorter-lived seeds than dominant forbs (Stampfli and Zeiter 2004), that have heavy seeds. Differences in the root systems of the grasses and forbs could also explain why forbs are dominant in low rainfall treatments. The deep root system of the forbs allows the forbs to access water and nutrients from the deeper soil layers, whereas on the other hand grasses have a shallow root system, hence they are not able to access water from the deeper soil layers (Nippert and Knapp 2007). In addition, in low rainfall interception treatments, i.e., 0% and

15% RI, grasses may likely over shade and outcompete the smaller forbs for resources such as light, soil nutrients and soil water (Van Coller *et al.* 2018).

The rainfall interception effect not only affects the aboveground biomass production and height but also modifies the species richness, diversity and functional group richness (Derner *et al.* 2011). It can be said that the deep root system of the forbs enables the competitive dominance of these species over grasses under moisture deficit conditions (Vine 2004; Suttle *et al.* 2007; Harrison *et al.* 2015). In this study, the forbs are outcompeted by grasses at 0% and 15% as the grasses dominated these plots because of adequate rainfall that was available to support the growth of the decreaser grasses that dominated at 0% and 15% rainfall interception and increaser grasses that dominated the 30% rainfall interception treatments. The decline in grass production with rainfall interception leads to a gradual build up in forb production, whereas the decline in forbs populations leads to grass build up (Vine 2004). Forbs perform better when there is weak grass competition whereas grasses are more responsive to rainfall. The differences in environmental favourability between grasses and forbs is as a result of the competition (Vine 2004).

Our results show that the longer resting periods in autumn resulted in less grass biomass production, which ultimately resulted in less overall aboveground biomass production, whereas the effect of resting on the forbs biomass production was not consistent. The pattern of variation in seasonal rainfall had a strong significant effect on the pattern of overall biomass production in both years. The 2016/17 spring and summer seasons had lower rainfall than the 2017/18 spring and summer seasons, whereas the 2016/17 autumn season had a higher rainfall than the 2017/18 autumn season (Figure 4.1). Hence, the vegetation height and biomass production of 2017/18 in spring and summer was higher compared with the same period in 2016/17, whereas in autumn of 2016/17 the biomass production was higher compared with 2017/18. These results concur with those reported by (Gremer *et al.* 2015), who reported that seasonal rainfall is an important driver of temporal dynamics of perennial grass richness. The overall biomass production was directly proportional to the rainfall amount received in each season as this was reflected through the biomass production where the overall biomass production was lower in the spring and autumn seasons of 2016/17 than the summer season in both years.

The results observed in this study could also suggest that interception in rainfall is not the only factor that plays a major role in terms of biomass production but its interaction with resting period and the season in which the rainfall interception occurs also matter a lot in affecting biomass production (Gremer *et al.* 2015; Huxman *et al.* 2004; Heisler-White *et al.* 2008; Weltzin *et al.* 2003). In this study, the summer season had the highest amount of rainfall in both years (2016/17 and 2017/18) and had the highest biomass production compared with the other two seasons (spring and autumn). The resting period of 90 days in the spring season in both years benefited plants by providing them enough time to recover from the physiological shock that might have been caused by cutting at the beginning of the spring season after winter and the low temperature of the winter season. The higher biomass at the 90-day resting period can be also partly attributed to grass flowering that occurred after the 70-day resting period as the flowering parts also add to biomass (Na *et al.* 2014). The biomass production was higher in summer than the spring and autumn seasons, which is because of the high summer rainfall during summer season in both years.

Overall biomass production decreases with the increase in rainfall interception. This trend agrees with the trend reported by (Snyman & Van Rensburg 1990), who reported higher biomass production in plots that did not experience rainfall interception than the ones that experienced severe rainfall interception treatments. Seasons alter biomass production and hence it is important that interpretation of the response take seasons into consideration to capture these differences that occur in different seasons. This is supported by the variability of the drought effect observed from season to season elsewhere (Chaves 2004). Annual seasonal rainfall patterns are the main drivers of rangeland ecosystem and its duration determines biomass yield (Heisler-White *et al.* 2008). This interception in rainfall is also accompanied by an increase in monthly average temperature which exceeded the 30 years monthly average temperatures of the study site for both years (Figure 4.8).

The rain use efficiency (RUE) was higher at the 90-day resting period in spring at all plots than the 70-day resting period in 2016/17, whereas in summer of both years the highest RUE was recorded for plots with the 70-day resting period rather than the 90 days one. Our results showed that biomass production is directly proportional to rain use efficiency as the grasses with higher RUE produced higher biomass. The RUE can also be used as a tool to determine biomass production. These results agree with those reported by (Mårtensson *et al.*

2017), who reported that water use efficiency coincides with the pattern of biomass production. This study was limited to biomass production as it is the harvestable biomass yield that is of primary interest for animal production.

The PCA showed that decreaser grass species that were dominated by *D. eriantha* were more abundant at 0% rainfall interception and 15% rainfall interception in both years. They are less competitive compared with the increaser species dominated by *E. curvula* under low rainfall conditions. This implies that decreaser grass species require more water to produce more biomass (Figures 4.7 and 4.8). In contrast, *E. curvula*, which is an increaser II grass species, was more dominant at 30% and 60% RD in 2017/18. Moreover, forbs produced more biomass at 60% rainfall interception, which means that they are able to better tolerate water stress compared with grasses (Figures 4.7 and 4.8). Forbs can also be an important source of forage in overgrazed and water stressed environments (Van Coller *et al.* 2018).

4.6. Conclusion

Rainfall interception associated with climate change poses a threat to the current rangeland productivity as it will lead to a decrease of forage biomass yield, as shown in this study. Decreaser grasses are most likely to be negatively affected by severe rainfall interception than increaser grasses and forbs. Although the grassland productivity has shown resilience to an interception in rainfall up to 15%, a severe interception will lead to changes in the herbaceous layer, which may lead to rangelands being dominated more by forbs than grasses beyond a 30% interception in rainfall. Within the grass species, increasers are more tolerant to rainfall interception than decreasers and thus are likely to increase with the decrease in rainfall beyond 15%. Resting the rangelands for at least 90 days or more compared with 70 days will improve rangeland biomass productivity during the spring and summer seasons, whereas there is no benefit of resting for 90 days compared with 70 days during autumn harvest. Further studies need to be conducted to quantify the impact of long-term rainfall interception on the growth pattern of key species, soil vegetation cover, soil nitrogen and carbon dynamics, soils seedbank and soil microbiota diversity to accurately model and predict the impact of reduced rainfall on the country's rangelands to create climate change adaptation strategies.

Chapter 5

Effect of rainfall interception and resting period on soil seed bank of grassland in Gauteng, South Africa

5.1. Abstract

It is forecast that climate change will affect soil seed banks (SSBs) through modifying aboveground vegetation species composition and plant fecundity. This study was conducted using split plot design to determine whether different intensities of rainfall interception and resting periods (70 and 90 days) had an effect on SSBs in South Africa. Rainfall interception was applied as main plot treatment at four levels (0%, 15%, 30% and 60%) using the rainout shelters, and the main plot treatments were each replicated five times. Resting periods were applied as split plot treatments. Four SSB samples of 8 cm diameter and 20 cm depth were collected from each plot and subplot treatment in 2018 and 2019. Seed emergence method was used to determine the SSB species composition and density. The 60% rainfall interception resulted in significantly high forb SSB densities in both years. In contrast, rainfall interception had no effect on grass SSB density in 2018, whereas grass densities were affected more significantly at 60% rainfall interception than 0% rainfall interception in 2019. The 90-day resting period resulted in significantly higher grass density than the 70-day resting period. Drought in the form of rainfall interception had a negative effect on grass SSB whereas it promoted forb SSBs

Key words: Climate change, densities, forbs, semi-arid grassland

5.2. Introduction

Climate change manifested in terms a decline in the amount of rainfall and general changes in rainfall patterns in particular facilitate the extinction of some herbaceous species, leading to rangeland degradation. This causes decline in herbaceous species diversity, forage production and seed production (fecundity). Under these circumstances, SSBs may serve as reservoir and gene banks to restore species diversity and maintain herbaceous populations, and as indicators of future communities (Vandvik *et al.* 2016). The regeneration success from SSBs following environmental disturbances (for example drought) and perturbations depends on their size and composition (Hu *et al.* 2019). Ecosystems across the world are affected by climate change, which will affect SSBs, as they are determined by the plants that are above the ground. The SSB is a repository for the next generation of plants, and consists of the seeds on the soil surface and within the soil (Hu *et al.* 2019). The SSB is important in grassland productivity as it is the basis for survival, population settlement, expansion and reproduction (Milberg & Hansson 1993). History and the current situation of a community are reflected in the SSB (Thompson 2000; Kalamees *et al.* 2012). Any factors that contribute to productivity of vegetation or to biodiversity and grassland degradation because of climate change could affect the size and the composition of the SSB (Dreber & Esler 2011; Báldi *et al.* 2013).

By allowing seeds into dormancy and therefore forming a seed bank, plants commonly delay their reproduction (Baskin & Baskin 1998). A reduced mean annual number of seedlings is the result of delayed germination, which is an apparent rainfall reduction (Baskin *et al.* 2002). Soil seed banks are an important aspect of grassland, as they determine its current and future condition. Seed recruitment from the SSB is restricted to soil parameters and periods with favourable conditions for seed germination (Solomon *et al.* 2006). Soil pH (Henig-Server *et al.* 1996), light (Trabaud & Renard 1999), soil water (Snyman 2004) and heat exposure (Snyman 2005a) are some of these important variables. According to Del Cacho *et al.* (2012), simulated climate experiments provide the best approach to studying the processes that determine the community changes at stand level.

It is essential to understand SSB current status under climate change to raise awareness and formulate management for future climate change-induced effects on vegetation. Climate manipulation may affect SSB when seed input is not depleted by germination because of unfavourable conditions imposed by climate modification (del

Cacho *et al.* 2012). Grassland researchers and scientists predict a reduction in cover and productivity owing to droughts (Hufkens *et al.* 2016; Basto *et al.* 2018), which may further affect SSBs negatively. However, some studies on climate manipulation show that these responses differ from community to community and in soil with different properties (Fridley *et al.* 2011). There is still a knowledge gap in SSB dynamics under climate change in semi-arid grasslands regarding the importance of SSBs in restoration and conservation of herbaceous populations and communities. Most rangeland studies in Africa focus on the aboveground vegetation community and ignore the SSB, which also requires attention. Therefore, this study was conducted to determine the overall effect of rainfall interception and resting period on SSB with the specific objective of examining the responses of forbs and grass composition and density in four rainfall interceptions (0%, 15%, 30% and 60%) and two resting periods (70 and 90 days).

5.3. Materials and methods

5.3.1. Site description

The study was conducted at Hatfield Experimental Farm, University of Pretoria. The farm is situated at an altitude of 1372 m above sea level. The coordinates of the study site are 25° 45' S and 28° 16' E. The farm is situated in a summer rainfall area with long-term mean annual rainfall of 674 mm. The soil on the farm is categorized as non-calcareous with a homogenous red colour, weak structure of Hutton form, and is sandy loam with 20–35% clay (Soil Classification Working Group 1991) and a pH of 6. The study site had not been grazed for more than 65 years. The research was conducted with rainout shelters as described by Yahdjian & Sala (2002) and modified by Talore (2015) constructed on natural semi-arid grassland vegetation, as described by Mucina & Rutherford (2006) to intercept 15%, 30% and 60% of ambient rainfall.

5.3.2. Rainout shelters and resting periods

Rainfall interceptions were employed as main plot treatment at four levels, namely 15%, 30%, 60% and 0% (control/ambient). The main plot treatments were each replicated five times using the rainout shelters arranged as main plot treatments in a split plot experimental design. The main plots were 49 m² (7 m x 7 m) and were covered by metal frame structures with V-shaped clear acrylic bands on top without ultraviolet filter. These plots were sub-divided into two sub-plots with two resting periods (70 and 90 days). A 25

cm ditch was excavated along the boundary of the experimental site to avoid water runoff into the plots. The bands were constructed with longitudinal plates at an angle of 120° , and a mean height of 1 m at the lowest side of the shelter was maintained. Water was collected from the acrylic material and channelled through the gutters away from the plots. Ambient rainfall was measured after each rainfall event using five rain gauges that were scattered over the experimental site.

5.3.3. Soil and soil seed bank sampling

The soil samples were collected in August 2018 and August 2019. These sampling periods occurred after the seed production event and before seed germination. According to Solomon *et al.* (2006), this would ensure that viable seeds did not germinate in the field over the season as the rains start in September. Four soil samples were taken per sub-plot (70- and 90-day resting period) using a soil auger. The four samples per sub-plot were bulked. The soil samples were 8 cm in diameter and 20 cm in depth (1005 cm^3). The samples were placed in plastic bags. The soil was passed through a 5-mm sieve to remove stones and roots, and was kept in a cold room while the space at the glasshouse was being prepared. Seed emergence was used to determine the SSB instead of seed separation, as this could have resulted in underestimation of densities owing to the very small size of seeds of species such as *Eragrostis curvula* (Leck *et al.* 1989; Baskin & Baskin 1998; Del Cacho *et al.* 2012).

Prior to placing soil samples in the germination trays, sterile filter sand was placed in the trays to increase rooting depth. The filter sand was irrigated for three weeks to assess seed contamination of the filter sand, but no seedling emerged. The soil samples were spread in thin layers of about 2 cm over the filter sand. The soil was kept in the trays for three months, namely September, October and November 2018 and 2019. Germination trays (20cm x 30 cm in size) were randomly placed in a glasshouse and were irrigated daily to maintain soil moisture at field capacity. Seedling emergence was recorded every second day from 01 September to 28 November 2018 and 2019, after which there was no emergence and hence a germination-stimulating chemical was used (15% ethanol) (Mdela *et al.* 2019). Some of the plants died at the seedling stage. These consisted of both forbs and grass seedlings. The grasses were identified as described by Van Oudtshoorn (2012). Forb species were identified at the South African National Biodiversity Institute (SANBI)

in 2018 (Table 6.1) and at the University of Pretoria Herbarium in 2019 (Table 6.2). Plants were identified at functional group level during emergence as they were almost impossible to identify at species level during the seedling stage.

Data were log transformed. Data for seed densities were analysed using the general linear model procedure (Proc GLM) of SAS (2008). The rainfall interceptions and the resting periods were the fixed effects, whereas the blocks were the random effects. Seedling emergence consisted of the number of seedlings that emerged per sampled area. The seedlings were separated into non-grasses (forbs) and grasses. Densities of the SSB on the sampled area and per square metre were analysed for forbs, grasses and total number of seedlings using Tukey's test at a confidence level of 95%.

Species diversity was calculated using Simpson's index (Yadav & Mishra 2013)

$$D = \frac{\sum ni(ni-1)}{N(N-1)}$$

Where D = diversity

n_i = total number of plant species of each individual species

N = the total number of all plant species.

5.4. Results

5.4.1. Soil seed bank composition

Rainfall interception reduced grass SSB species abundance in 2019. On the other hand, reducing the resting period reduced the grass SSB in 2019 (Table 5.1). The grass SSB was lower at 60% rainfall interception. Moreover, the 90-day resting period resulted in higher grass SSB abundance than 70 days resting in 2019. The grass SSB abundance decreased by 39.4% at 60% rainfall interception compared with 0% rainfall interception in 2019. Rainfall interception had a significant ($P < 0.05$) effect on forb abundance in 2018 and 2019 (Table 5.2). On the other hand, the resting period had no significant effect on forb abundance in 2018, whereas it had a significant effect in 2019. Forb abundance was ($P < 0.05$) higher at 60% rainfall interception compared with 0% rainfall interception in both years. Forb abundance increased by 63.5% and 45.5% at 60% rainfall interception compared with 0% rainfall interception in 2018 and 2019, respectively. On the other hand,

the 70-day resting period resulted in significantly high forb abundance compared with 90 days in 2019.

Table 5.1 Abundance (%) species in the soil seed bank under different rainfall interception levels in 2019

Species	Functional group	Ecological status	70 days resting period				90-day resting period			
			Rainfall interception				Rainfall interception			
			0%	15%	30%	60%	0%	15%	30%	60%
<i>Bidens pilosa</i>	Forb	Invader	0	3.1	3.6	5.8	4.0	0	2.7	6.9
<i>Brassicaceae</i> spp.	Forb	Invader	0	0	3.6	0	0	0	0	0
<i>Chenopodium carinatum</i>	Forb	Invader	5.5	0	3.6	0	0	0	0	0
<i>Conyza fleabane</i>	Forb	Invader	9.2	3.1	7.1	23.2	4.0	7.9	5.4	6.9
<i>Cynodon dactylon</i>	Grass	Increaser II	5.5	3.1	0	11.6	4.0	9.8	5.4	6.9
<i>Cyperus rotundus</i>	Sedge	Invader	8.3	3.1	0	0	0	7.9	19.0	6.9
<i>Digitaria eriantha</i>	Grass	Decreaser	16.6	5.5	7.1	0	9.9	9.4	10.2	6.9
<i>Eragrostis curvula</i>	Grass	Increaser II	18.8	35.4	35.7	18.8	29.7	25.1	32.0	22.1
<i>Eragrostis lehmanniana</i>	Grass	Increase II	0	6.3	3.6	5.8	5.0	9.4	2.7	6.9
<i>Euphorbia inaequalis</i>	Forb	Invader	0	0	3.6	0	0	0	0	0
<i>Gamochaeta pensylvanica</i>	Forb	Invader	0	0	3.6	0	4.0	0	0	0
<i>Heteropogon contortus</i>	Grass	Increaser II	0	6.3	0	0	0	0	0	0
<i>Melinis repens</i>	Grass	Increaser II	0	0	14.3	0	4.0	0	0	0
<i>Nidorella resedifolia</i>	Forb	Invader	5.5	6.3	0	11.6	4.0	3.9	4.1	8.7
<i>Oxalis corniculata</i>	Forb	Invader	11.1	0	0	5.8	0	0	8.2	6.9
<i>Phyllanthus</i> spp	Forb	Invader	5.5	3.1	0	0	0	0	0	0
<i>Portulaca quadrifida</i>	Forb	Invader	0	3.1	0	0	0	0	0	0

<i>Sonchus oleraceus</i>	Forb	Invader	5.5	3.1	3.6	0	0	3.9	0	0
<i>Tagetes minuta</i>	Forb	Invader	0	3.1	0	0	0	3.9	0	0
<i>Taraxacum officinale</i>	Forb	Invader	0	3.1	0	0	4.0	3.9	3.4	0
<i>Themeda triandra</i>	Grass	Decreaser	0	3.1	0	0	15.8	7.9	0	0
<i>Urochloa mosambicensis</i>	Grass	Increaser II	0	0	3.6	0	0	0	0	0
<i>Verbena aristigera</i>	Forb	Invader	0	0	0	0	0	0	2.7	0
<i>Verbena officinalis</i>	Forb	Invader	8.3	8.8	3.6	17.4	7.9	6.5	4.1	20.8
<i>Wahlenbergia undulata</i>	Forb	Invader	0	0	3.6	0	4.0	0	0	0
Total abundance of forbs (%)			50.7	37.1	35.7	63.8	31.7	30.1	30.6	50
Total abundance of grasses (%)			41.0	59.7	64.3	36.2	68.3	62.0	50.3	42.9
Total abundance of sedges			8.3	3.1	0	0	0	7.9	19.0	6.9
Number of species (species richness)			11	16	14	8	13	12	12	10

Table 5.2 Effect of rainfall interception and resting period on forb soil seed bank abundance (%) in 2018 and 2019

Parameter	DF	2018	2019
	3	0.0053***	0.0315*
Rainfall interception			
0%		47.06 ± 5.58 ^c	46.39 ± 3.33 ^b
15%		58.05 ± 6.35 ^b	41.53 ± 3.33 ^b
30%		65.77 ± 6.07 ^{ab}	40.25 ± 3.33 ^b
60%		76.99 ± 5.26 ^a	67.47 ± 3.33 ^a
Resting period	1	0.2069NS	0.0001***
70 days		58.19 ± 4.23	52.65 ± 2.35 ^a
90 days		65.74 ± 4.02	45.17 ± 2.35 ^b
RI*RP	3	0.1779NS	0.0555

Different superscripts along the same column were significantly different

NS: non-significant at $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; DF: degree of freedom; RI: rainfall interception; RP: resting period

Different superscripts along the same column were significantly different

5.4.2. Forb soil seed bank densities

The interaction of resting period and rainfall interception had no significant effect on forb SSB densities in 2018 and 2019 (Table 5.4). Forb SSB densities increased with the increase in rainfall interception. The SSB densities of forbs increased by 176% and 26% at 60% rainfall interception compared with 0% rainfall interception in 2018 and 2019, respectively (Figures 5.1a and 5.1b). Resting period had no significant effect on forb SSB densities per square metre, whereas rainfall interception had a significant effect in both years

Table 5.3 ANOVA table showing the effect of resting period, rainfall interception and their interaction on total densities per square metre

Significance (p-value)			
Year	RI	RP	RI*RP
DF	3	1	3
2018	0.0002***	0.3212NS	0.2233NS
2019	0.0597*	0.8122NS	0.6075NS

NS: non-significant at $P > 0.05$; * $P < 0.05$; ** $P < 0.01$, *** $P < 0.001$

DF: degree of freedom, RI: rainfall interception, RP: resting period

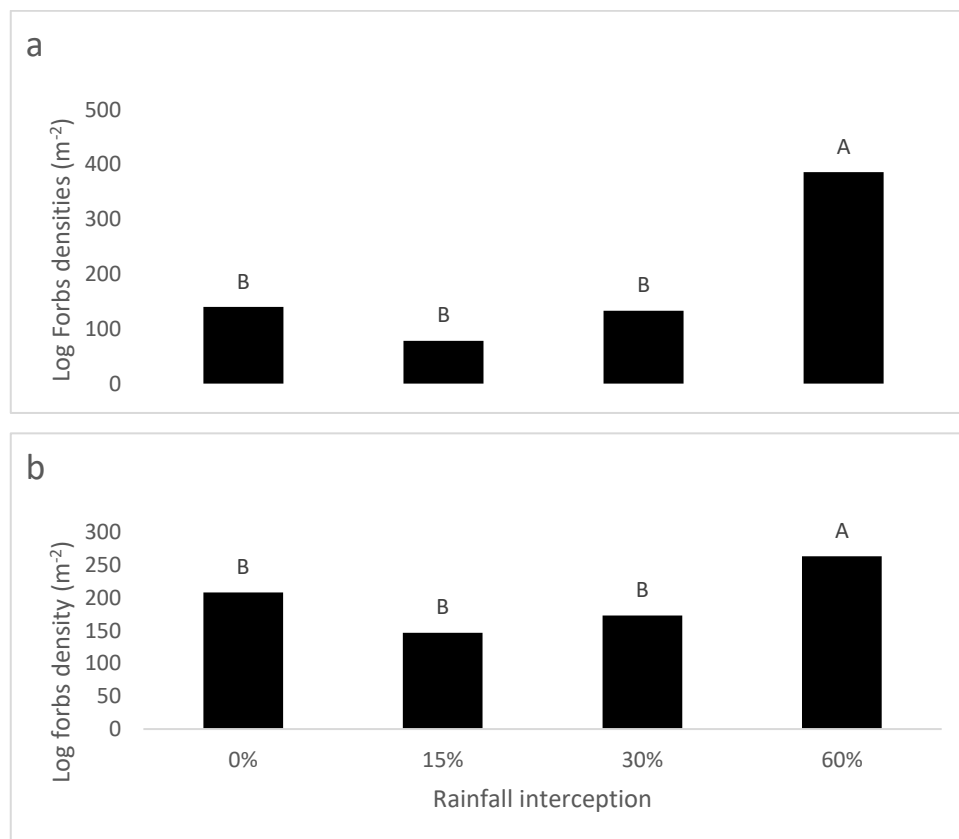


Figure 5.1 Effect of rainfall interception on forb seed densities per square metre in (a) 2018 and (b) 2019. Different letters were significantly different.

5.4.3. Grass soil seed bank densities

The interaction of rainfall interception and resting period had no significant effect on grass SSB densities in 2018 or 2019 (Table 5.4). However, in 2019 resting period and rainfall interception both had significant effects on grass SSB densities. Although rainfall interception had no significant effect on grass SSB density in 2018, it appears that there

was a reduced grass SSB by 21% at 60% rainfall interception compared with 0% rainfall interception. Moreover, in 2019 rainfall interception reduced grass SSB density by 52% at 60% rainfall interception compared with 0% rainfall interception whereas 90-day resting period resulted in significantly high grass SSB density compared with the 70-day period.

Table 5.4 Effect of rainfall interception and resting period on grass seed densities per square metre in 2018 and 2019

Parameter	DF	2018	2019
Rainfall interception	3	0.8838NS	0.0049**
0%		145.4±28.18	261.7±29.22 ^b
15%		123.3±26.57	350.0±29.22 ^a
30%		118.3±26.57	273.3±29.22 ^{ab}
60%		118.3±26.57	125.0±29.22 ^c
Resting period	1	0.3733NS	<0.0001***
70 days		138.5±19.37	208.3±20.66 ^b
90 days		114.2±18.79	296.7±20.66 ^a
RI*RP	3	0.2942NS	0.1828NS

NS: non-significant at $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; DF: degree of freedom; RI: rainfall interception; RP: resting period. Different superscripts along the same column were significantly different

5.4.4. Total densities per square metre

The interaction of rainfall interception and resting period was not significant on total SSB densities ($P=0.4559$ in 2018 and $P=0.6948$ in 2019) (Table 5.5). Resting period had no significant effect on total SSB densities in 2018 either, whereas it did have an effect on total SSB densities in 2019. However, rainfall interception had a significant effect on total SSB density in 2018. Total SSB densities were higher at 60% rainfall interception in 2018, whereas they were higher at 15% rainfall interception in 2019 compared with 0% rainfall interception (Figure 5.2a and 5.2b). In 2018, the total SSB density was increased by 78% at 60% rainfall interception, whereas it increased by 27% at 15% rainfall interception in 2019 compared with 0% rainfall interception.

Table 5.5 ANOVA table showing the effect of resting period, rainfall interception and their interaction on total densities per square metre

Significance (p-value)			
Year	RI	RP	RI*RP
DF	3	1	3
2018	0.0117*	0.8736NS	0.4559NS
2019	0.0684NS	0.0153**	0.6948NS

NS: non-significant at $P > 0.05$; * $P < 0.05$; ** $P < 0.01$, *** $P < 0.001$

DF: degree of freedom, RI: rainfall interception, RP: resting period

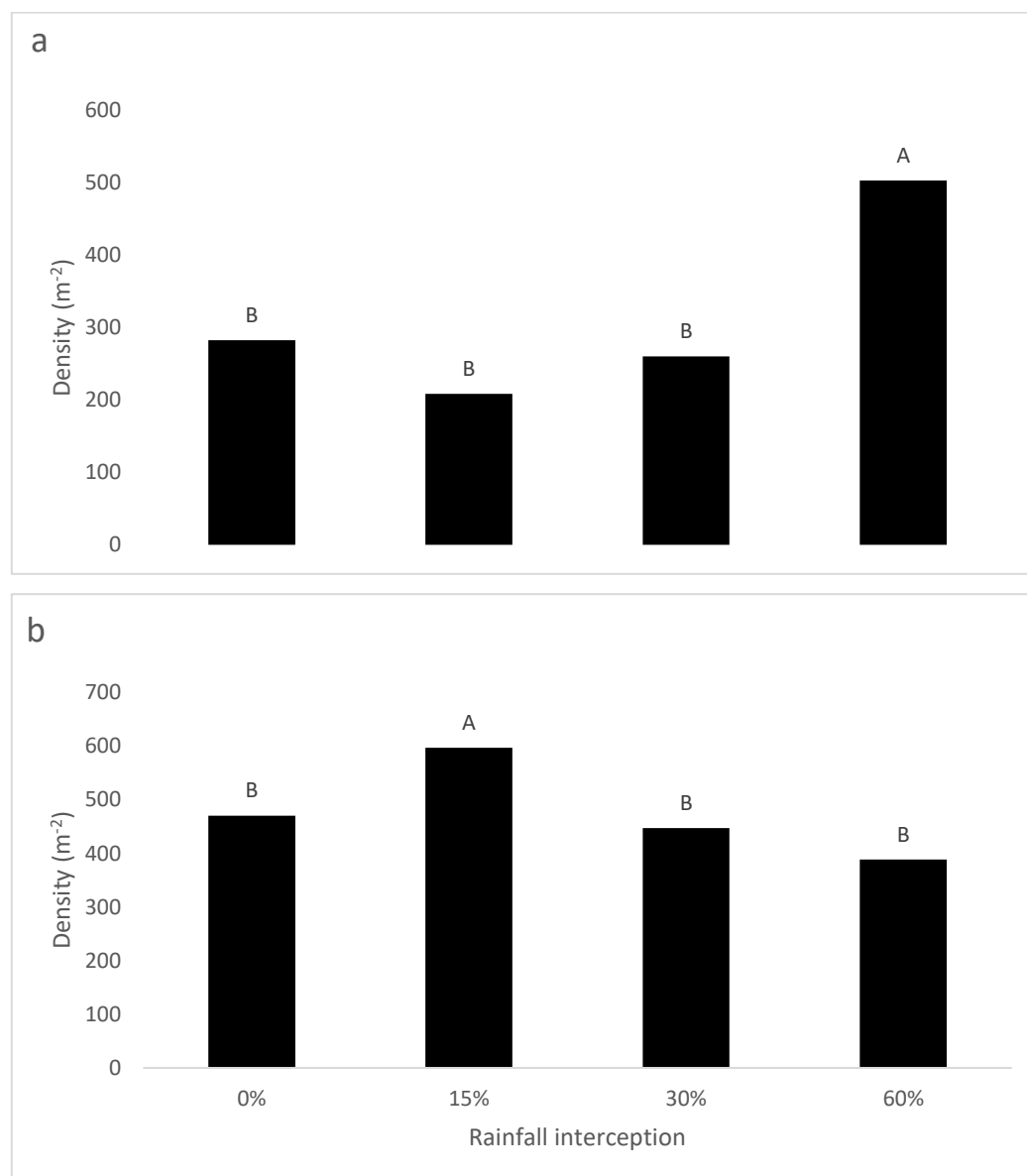


Figure 5.2 Total soil seed bank densities (m⁻²) as determined by rainfall interception in a) 2018 and b) 2019. Different letters are significantly different.

5.4.5. Species richness as influenced by rainfall interception in 2019

Rainfall interception and resting period had no significant interaction effect on SSB species richness in 2019 (Table 5.6). Moreover, resting period had no significant effect on SSB species richness. On the other hand, rainfall interception had a significant effect on SSB species richness in that it led to reduced species richness because 60% rainfall interception resulted in lower SSB species richness compared with 0%, 15% and 30% (Figure 5.3).

Table 5.6 ANOVA table showing the effects of resting period, rainfall interception and their interaction on soil seed bank species richness in 2018

	RI	RP	RI*RP
DF	3	1	3
<i>P</i> -value	0.0324*	0.1336NS	0.6347NS

NS: non-significant at $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

DF: degree of freedom; RI: rainfall interception; RP: resting period

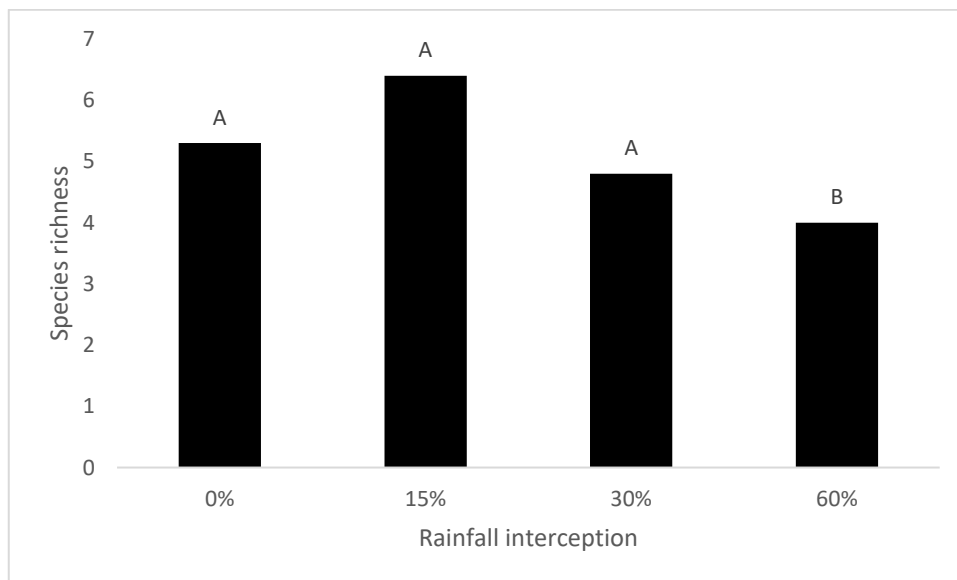


Figure 5.3 Mean soil seed bank species richness as determined by rainfall interception in 2019. Different letters were significantly different.

5.4.6. Species diversity as determined by rainfall interception

Rainfall interception and resting period had no significant interaction effect on the species diversity (Table 5.7). Moreover, resting period did not result in a significant effect

on species diversity. However, rainfall interception had a significant effect on SSB species diversity. The 30% rainfall interception resulted in high species diversity compared with 0%, 15% and 60% rainfall interception (Figure 5.4).

Table 5.7 ANOVA table showing the effect of resting period, rainfall interception and their interaction on soil seed bank species richness in 2019

	RI	RP	RI*RP
DF	3	1	3
P-value	0.0402*	0.5280NS	0.4160NS

NS: non-significant at $P > 0.05$; * $P < 0.05$; ** $P < 0.01$, *** $P < 0.001$

DF: degree of freedom, RI: rainfall interception, RP: resting period

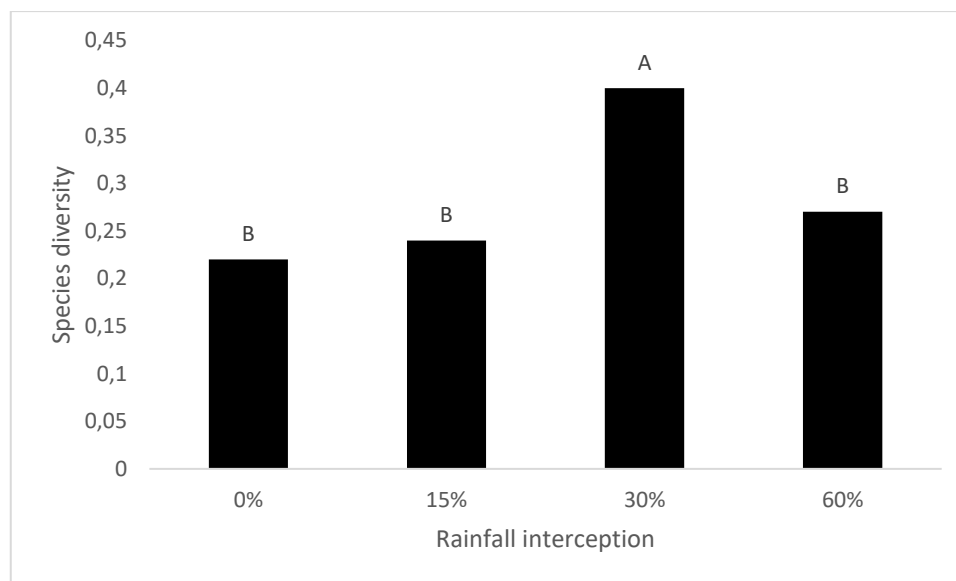


Figure 5.4 Mean soil seed bank species diversity as determined by rainfall interception in 2019. Different letters were significantly different.

5.4. Discussion

A total of 25 plant species, of which six grass and 18 forbs and one sedge were recorded in the SSB in 2018 and 2019 (Tables 6.1). Soil seed bank densities for forbs increased exponentially as rainfall interception increased, indicating that the germination requirements of some seeds had not been met because of decline in soil moisture as rainfall was intercepted, which led to the accumulation of seeds over time, adding to the previous

year's SSB. This highlights that seeds at higher rainfall interception maintain their viability for a long time, probably owing to extended dormancy. Conversely, at low rainfall interception, more seeds are likely to germinate every rainy season, thereby depleting the SSB size. The findings of this study suggested that vegetation restoration was possible, even after consecutive severe rainfall interceptions (drought) but it would probably be initiated by forbs rather than grasses because of higher forb density. Thus, for grazing purposes, rangelands might require some sort of re-enforcement through reseeding by drought-tolerant grasses such as *Eragrostis curvula* and *E. lehmanniana* to fast-track desirable vegetation recovery. In other studies in which grazers were not involved, perennial grasses started to dominate. This resulted in a rapid decline in species diversity (Sykora *et al.* 1990; Hill *et al.* 1992; Snyman 2004).

The 90-day resting period had higher grass abundance than the 70-day period in 2019, whereas the resting period had no significant effect on grass SSB abundance in 2018. This could be because the 70-day harvest took place before the grasses dropped their seeds, whereas the 90-day harvest took place afterwards. This resulted in the 70-day resting period having a lower grass SSB than the 90-day resting period, whereas resting period had no significant effect on grass SSB in 2018. These results concurred with those reported by Beier *et al.* (2004) that the SSB fell at drought treatments compared with control, probably because of an indirect water deficit. These treatments affected the vegetation, which led to a decrease in grass productivity on high rainfall interception treatment (60%), whereas forbs increased with the interception in rainfall (Figure 6.1) because most forbs have deeper root system than grasses. These forbs dropped their seeds, which contributed to a large degree to the SSB. The findings of the current study are in contrast to those of Akinola *et al.* (1998a, b), who found that rainfall interception rarely affected SSB.

Water availability limits plant growth in the ecosystem (Larcher 2000), and difficulties in plant growth and survival could be exacerbated by drought (Llorens *et al.* 2004; Prieto *et al.* 2009). Ultimately seed production would be affected (Del Cacho *et al.* 2012). However, the current rainfall interception treatments did not completely exclude soil moisture, but reduced its availability relative to the ambient rainfall. Consequently seedlings were able to emerge after rainfall events. This could affect the full plant reproductive cycle by delaying seed production (Del Cacho *et al.* 2012). The experiment might have cumulative effects if continued over several years, resulting in a significant

decrease in SSB of grasses and more forbs at high rainfall interception compared with control. This concurs with results reported by Akinola *et al.* (1998a), who argued that annual species, which are mostly forbs, respond faster to climate manipulation.

Many studies reported large persistent SSB on rangelands (Milberg & Hansson 1993; Edwards & Crawley 1999), where in most cases belowground species composition differed from aboveground (Snyman 2004). In the current study, the results showed lower densities of SSB, especially at the 0% and 15% rainfall interception treatments for 2018, whereas the opposite was true of 2019 (Figure 5.2a). The high seedling density of forbs in both years correlated with high rainfall interception (60%). This agreed with the findings of Snyman (2004), who reported slightly larger SSB production on degraded rangeland. Rainfall interception leads to bare patches at 60% rainfall interception, which produce land degradation as a result of soil erosion because of lower soil cover. Few decreaser grass species such as *Digitaria eriantha* and *T. triandra* were recorded at low rainfall interception compared with high rainfall interception treatments. The absolute SSB composition could be important in determining the future conditions of rangeland and dictating which species would play a part in successional processes (Kinucan & Smeins 1992; Snyman 2004). In the current study the total densities per square metre increased at 60% rainfall interception in 2018 and at 15% rainfall interception in 2019 (Figures 5.2a and 5.2b).

Sampling methods are decisive when conducting comparative SSB studies. They must include soil depth, sample size, number of germination cycles, seasons and the involvement of grazing animals. Soil seed bank densities from the current study (282.74, 208.60, 260.32 and 503.41 total seedlings m^{-2}) for 0%, 15%, 30% and 60% rainfall interception, respectively, were within the ranges reported in South Africa, namely 200 seeds m^{-2} in KwaZulu-Natal (Adams 1996), and 350 seeds m^{-2} of *T. triandra* (O'Connor 1997), but were lower than those from USA, namely 800 m^{-2} in southern Arizona (Ruyle *et al.* 1988), and 2 252 to 4 409 seeds m^{-2} in Texas (Kinucan & Smeins 1992).

The 60% rainfall interception treatment had more bare patches than the other treatments. Seed predators such as ants play a pivotal role in predation and seed dispersal, whereas the vegetation determines the composition of ant communities and structure (Arnan *et al.* 2006). These ants were more visible at the 60% rainfall interception than at

0%, 15% and 30% (personal observation). This agrees with the findings of Arnan *et al.* (2006) and Rodrigo & Retana (2006), who reported an abundance of ants under low vegetation cover, and those of Wolff and Debussche (1999), who reported a decline in the number of ants as the vegetation cover increased. According to Del Cacho *et al.* (2012), ant activities may increase in plots with larger bare patches because of water deficit, which hampers the regeneration of vegetation, leading to increased seed removal. However, ants may bring seeds from outside the plots, but this would be minimal, as there was no visual observation of high densities of ants outside the 60% rainfall interception treatments. However, these bare patches reduced the densities of grass seedlings and increased those of forbs. There might be reasons for these termites preferring grass seeds to those of forb plants for example because of size.

Basto *et al.* (2018) reported that grass seeds in calcareous grassland soils were not viable long-term summer drought. This might explain why there were no major differences between the aboveground vegetation and the SSB, since the grass seeds might have died because the experiment had been running continuously for more than five years (Talore 2015). The decline in a grass abundance in the SSB varies with soil water content and grass species, whereas forb species increase in an SSB as the soil moisture decreases (Gazanchian *et al.* 2006; Rohollahi *et al.* 2015). Reduced soil moisture also influenced the availability of soil nutrients that were required by plants (Köhler *et al.* 2001). For example, some species that grow in dry grassland soils have lower nitrogen uptake (Durand *et al.* 2010). Nitrogen might accumulate in the soil and affect the SSB (Basto *et al.* 2015a) and soil pH (Carroll *et al.* 2003), which could result in seeds being persistent in grassland soils (Basto *et al.* 2015b). Even a one-year drought may have long-term effects on grasslands that are unpredictable (Haddad *et al.* 2002).

5.6. Conclusion

The current results showed that rainfall interception had a negative effect on abundance and density of the grass SSB, whereas it improved the forb SSB. Moreover, rainfall interception might eventually affect seed storage in the soil, which plays a pivotal role in grassland plant dynamics. Rainfall interception affected the SSB of the most palatable species such as *T. triandra* and *D. eriantha* negatively. These species were fewer in the SSB from 60% rainfall interception compared with the ambient, because they did

not produce seeds at 60% interception. Therefore rainfall interception might lead to grasslands being dominated by forbs, resulting in larger bare patches that exposed the land to a possible degradation through soil erosion. Forbs seemed to be suppressed by grasses at lower rainfall interception treatments. However, the authors recommend that more studies of this nature be conducted, taking into consideration the effect of time lags between SSB collections. This calls for alternative interventions that could be considered if the droughts became more persistent, for example reseeding rangelands with natural occurring grasses in a specific area.

Chapter 6

6.1. General conclusion and recommendations

South African livestock farmers rely on natural rangeland for their livestock grazing. However, the effects of climate change such as drought make it difficult for farmers to thrive under these conditions. Reduced rainfall is likely to affect rangeland productivity and production negatively. This poses an increasing challenge to rangelands and users. Quantifying the impact of reduced rainfall and finding ways to mitigate these challenges are of paramount importance. Rangeland users also need to understand the importance and the duration of resting periods.

This study evaluated the impact of rainfall interception and resting period on semi-arid grassland species composition, herbaceous biomass yield, SSBs, and soil properties of semi-arid grassland subjected to various levels of rainfall interception and resting period. It was observed that vegetation height correlated positively with biomass. The current results showed that reduced rainfall had a significant effect on soil water content. The lowest soil water content was recorded at 60% rainfall interception. This means that with greater forecast reduction in rainfall soil will be much drier. The results also showed that more soil nutrients will remain on the top soil with less rainfall as the soil nutrients will not dissolve and percolate to the deeper layers of the soil. The study also showed that rainfall interception will affect the soil seed bank as some of the grass species would not be able to germinate owing to lack of soil moisture. The results demonstrated how the rangelands would look during and after the events of extended reduced rainfall. Vegetation diversity was most affected more at 30% and 60% rainfall interception than at 0% and 15%. Season also affected height because seasons with higher rainfall resulted in taller vegetation than those with lower rainfall.

There was a variation in biomass production over resting periods and seasons. Shorter resting periods improved grass biomass production in autumn, whereas longer resting periods improved grass biomass production in spring. The 60% rainfall interception had the lowest grass biomass production in all three seasons in both years compared with 0%, 15% and 30% rainfall interception. Dominant grasses species such as *Digitaria eriantha* and *Eragrostis curvula* contributed to greater grass biomass production than the less dominant grasses such as *Aristida congesta* and *Melinis repens* (Magandana *et al.* 2020). Overall biomass production was reduced significantly at 60% rainfall interception compared with 0%. The grassland showed resilience by making adjustments in species composition up to 30% rainfall

interception. However, a severe interception in rainfall amount at 60% and beyond would lead to lower biomass production in grassland biomes.

This would lead to fodder reduction, which would cause poor livestock performance because most beef farmers rely on natural grazing land and should promote growth of drought tolerant grasses such as *E. curvula* to produce enough forage during low to moderate intensity rainfall interception. Increaser grass species are more favourable for those conditions than decreaser grass species such as *D. eriantha* and are able to produce more biomass per unit of rainfall. It can be recommended that grasslands can be reseeded with *E. curvula* seeds. Moreover, it is important to avoid overgrazing as this will modify competition between grasses and forbs to the advantage of the forb functional groups, which may lead to less feed available for animals. Increaser species are more adapted to low soil moisture than decreaser species. Increaser grass and forbs species are more drought tolerant than decreaser grass species. Therefore, increaser grass species would be more tolerant to predicted future rainfall interception scenarios than decreaser grass species.

Forage in the arid and semi-arid areas of the sub-Saharan Africa is sensitive to rainfall interception. Sub-Saharan Africa rangelands are susceptible to climate change. Season plays a major role in overall biomass production as summer had higher biomass production than autumn and spring in both years. Higher temperatures and rainfall also play a role in higher biomass production in summer than autumn and spring. The high rainfall amount in 2016/17 resulted in higher cumulative biomass production than 2017/18. This means that with the future predicted decrease in rainfall, farmers will have to destock or supplement their animals where possible as the natural grazing lands will be negatively affected. The authors suggest that rangeland managers should be aware of the consequences of reduced rainfall and grazing and resting periods on their rangelands and be adjusted accordingly. They should always measure the carrying capacities of their rangelands and destock where possible to avoid overstocking and overgrazing. They should cull stock that is unproductive and, by so doing, they will be reducing grazing pressure.

6.2. Implications and recommendation for future research

This study looked at the impacts of reduced rainfall and resting period on rangeland productivity on aboveground biomass production and soil properties. It also evaluated how rangelands will respond to rainfall interception and resting periods. It determined how the rainfall interception will affect ecological groups (grasses and forbs). Such information could be used on climate models to predict the impact of climate change and warn against the effects of future drought. This will be useful in planning for future droughts in the long term. Better planning and mitigation strategies may come with the utilization research results based on this rainfall interception and resting period study. Information provided by the results of this study will make it clearer and easier for the rangeland managers to mitigate the impacts of future droughts on rangeland productivity. Rainfall reduction will negatively affect the farmers as they will have to buy more feed for their animals with the decrease in the available aboveground biomass. These changes could worsen as they multiply. Managers who know how these interactions work are likely to make better informed decisions. These decisions involve the types and numbers of animals that can be kept on a particular camp. These will include destocking on overstocked rangelands to avoid overgrazing.

This study showed that forbs are more likely to dominate the rangelands under reduced rainfall. More palatable grasses such as *Digitaria eriantha* and *Themeda triandra* are more likely to be negatively affected by reduced rainfall than increaser grasses such *Eragrostis curvula* and *Cynodon dactylon*. Reduction in rainfall will also require farmers to select animals that have high feed conversion ratio. We also evaluated the way in which the nutrient content these rangelands will be affected by reduced rainfall. Most nutrient contents were higher at 60% rainfall interception and 90-day resting period.

Availability of forage could be reduced with severe reduction in rainfall, but because of reduced residual soil water supply, the grassland may become sweet veld because of restricted growth and biomass accumulation and lignification of the herbage. Hence, there is a need to adjust the stocking rate of animals through destocking to match reduced carrying capacities of the grazing lands and farmers will be required to destock. Food security will also be negatively affected by this reduction in rainfall as animal products such as milk, meat and wool will be negatively affected. This could lead to more rangelands becoming sweet veld.

Furthermore, there will not be enough feed for animal production, which will further lead to lower animal production and productivity.

Future studies should look at the impact of reduced rainfall on the individual plant species. Another important limitation in this research, which is common to other studies conducted in short time scales, is that responses of plants vary from season to season and year to year, whereas the ecological response to rainfall changes over a long period is likely to be more complex. This is also true particularly of heterotrophic respiration, which is affected by moisture-deficit-induced reductions in soil fertility and nutrients as a function of reduced ANPP. Knowing all this will make it easier for rangeland users to manage predicted impacts of drought.

More studies that investigate the impact of increased temperature and elevated carbon dioxide are required to predict how the rangeland will react to such forecast temperature increases. There is also a need for research that will investigate the impact of these forecast changes on vegetation nutrient composition. Researchers should also conduct research to produce livestock breeds with high feed conversion ratio that can thrive on reduced forage on natural rangelands because of reduced rainfall.

6.3. Critical evaluation

The study was conducted over a short period (2016/17 and 2018/19) although the shelters were installed in 2013. The results are based on this period, but could give different results if they were based on a period such as five to fifteen years. Moreover, the involvement of animals could show which breeds would do best under limited grazing as a result of rainfall interception. The other shortcoming of this study was that the plant nutrient composition was not determined. One of the reasons that the study was conducted over a short time was because the PhD study had a duration of three years. However, this PhD took longer to finish because of the Covid-19 pandemic, which led to the total shutdown of the country. The laboratories were closed for the better part of the study period, which made it difficult to obtain the results in time. Moreover, funding was a challenge, which made it difficult to conduct experiments such as the effect of elevated carbon dioxide and temperature on grass species because these would be conducted in a closed environment with controlled temperature and carbon dioxide.

The soil seed bank was conducted over two years. With more years of research this might have given better insight into the effects of reduced rainfall interception. The deeper layers of the soil could also give more insight into the influence of rainfall interception on soil seed bank.

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