# EFFECTS OF CLIMATE AND LAND-USE CHANGE ON GRASS AND TREE POPULATIONS AND THEIR CONSEQUENCES TO THE ECOSYSTEM MULTI-FUNCTIONALITY, LIMPOPO, SOUTH AFRICA

by

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THESIS

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## DECLARATION

I declare that the thesis that I am submitting to the University of Limpopo for the degree of Doctor of Philosophy in Agriculture (Plant Production – Rangeland Ecology) is an original account of my study, that it was written by me, and that it has not been submitted previously for any degree or professional qualification, at this or any other university. The experimental work is almost exclusively mine; the collaborative contributions have been indicated clearly and acknowledged. All supporting literature and resources have been adequately referenced.

Mokoka M.V. 12 October 2022

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SALL net

DAAD
Deutscher Akademischer Austausch Dienst
German Academic Exchange Service

NRF
National
Research
Foundation

Universität Potsdam

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## LIST OF ACRONYMS

| | |
|---|---|
| ANOVA | Analysis of Variance |
| ANPP | Aboveground Net Primary Production |
| CBD | Convention on Biological Diversity |
| ES | Ecosystem Services |
| GLM | Generalized linear model |
| GO | Grazing offtake |
| GRA | Grazed plot |
| IDH | Intermediate Disturbance Hypothesis |
| IPCC | Intergovernmental panel on climate change |
| LA | Leaf Area |
| LDMC | Leaf Dry Matter Content |
| LEK | Local Ecological Knowledge |
| LNC | Leaf Nutrient Content |
| LSU | Large Stock Unit |
| LTE | Long-Term Ex-closure |
| NPP | Net Primary Production |
| NS | Non-significant |
| PFT | Plant Functional Type |
| SLA | Specific Leaf Area |
| STE | Short-Term Ex-closure |

## LIST OF SYMBOLS AND ABBREVIATIONS

| | |
|---|---|
| D+ | Drought conditions |
| D- | Non-drought conditions |
| $D+^{p}$ G- | Post-drought and continued resting |
| $D+^{p}$ $G+^{p}$ | Post-drought and post-grazing |
| $D+^{p}$ G+ | Post-drought and continued grazing |
| D- $G+^{p}$ | Continued ambient conditions and post-grazing |
| $FR_{ci}$ | Functional Richness |
| $FD_{var}$ | Functional Divergence |
| G- | Ungrazed vegetation |
| G+ | Grazed vegetation |
| H’ | Shannon-Wiener Index |
| Ha | Hectare |
| Hglan | Broad-leaved perennial grasses |
| Hglin | Narrow-leaved perennial grasses |
| Hgova | Very broad-leaved perennial grasses |
| *Indval.g* | Indicator value index |
| In prep. | In preparation |
| J | Pilou evenness |
| Lsmeans | Least squares Means |

## LIST OF PUBLICATIONS

### Peer-reviewed articles from the thesis

1. **Mokoka, M.V.,** Jordaan, J.J. and Potgieter, M.J., 2018. Correlations between growth parameters and establishment of *Vachellia tortilis* (Forssk.) Hayne populations in the Limpopo Province, South Africa. African Journal of Ecology. https://doi.org/10.1111/aje.12515

### Articles in preparation from the thesis

1. **Mokoka, M.V.,** Behn K, Mudongo E, Ruppert J, Ayisi K.K., and Linstädter A (in prep). What characterizes winner and loser species? Effects of severe drought and grazing on a dryland grassland.
2. **Mokoka, M.V.,** Behn K, Mudongo E, Ruppert J, Ayisi K.K., and Linstädter A (in prep). Effects of drought, grazing and resting on the taxonomic and functional diversity of Limpopo's dryland grasslands.

### National conference(s) attended and presented part of the thesis

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1. **Mokoka, M.V.,** Behn K, Mudongo E, Ruppert J, Ayisi K.K., and Linstädter A. Managing ecosystem functions and services in the face of drought: A plant functional trait perspective. The 62nd Symposium of the IAVS . University of Bremen – Bremen, Germany, July 19th 2019.
2. **Mokoka, M.V.,** Behn K, Mudongo E, Ruppert J, Ayisi K.K., and Linstädter A. What characterizes winner and loser species? Effects of severe drought and grazing on a dryland grassland. GFÖ virtual annual meeting. Virtual attendance, 30th of August to 1st of September 2021.

## THESIS STRUCTURE

The thesis's chapters are organized as follows:

**CHAPTER 1**

General Introduction
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This section addresses the background on climate and land-use change and their impact on semi-arid savanna, ecosystem services and the ecosystem's multi-functionality. Moreover, this chapter highlights the problem statement, aim, motivation, objectives, and hypotheses of the study.

**CHAPTER 2**

Literature Review
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This chapter provides a survey of the pertinent literature. The literature review is concerned with variables affecting the ecosystem's multi-functionality, particularly in the context of changing climate and land-use, in order to identify knowledge gaps.

**CHAPTER 3**

Research Methodology: The DroughtAct Experiment

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In this chapter the materials and methodology utilized in this study are described in detail. Furthermore, the rationale and justifications for the methodology is provided.

**CHAPTER 4**

What characterizes winner and loser species?
Effects of severe drought and grazing on a dryland grassland

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This section presents the DroughtAct experiment, which combines severe prolonged drought treatments with grazing treatments and evaluates ecosystem function and service provision from grazed and non-grazed vegetation under drought and ambient rainfall conditions. Specifically, the research studied the traits of the winning and losing species and plant functional types under long-term drought and moderate grazing. The experiment's overarching objective was to identify those species and plant functional types which are most vulnerable to drought.

**CHAPTER 5**

Effects of drought, grazing and resting on functional and taxonomic diversity
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In Chapter 5, effects of drought and grazing on functional and taxonomic diversity were evaluated under the DroughtAct experiment. Vital rates, cover and biomass of herbaceous species were recorded and compared between treatments.

**CHAPTER 6**

Correlations between growth parameters and establishment of *Vachellia tortilis* (Forssk.) Hayne populations in the Limpopo province, South Africa
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This chapter investigates the relationship between growth parameters and establishment of *Vachellia tortilis* (Forssk.) Hayne populations in the in the Limpopo province, South Africa. It is a dendrochronological study designed to discover the key drivers of ecological processes affecting tree establishment, how they have functioned historically, and how they could function in the future.

**CHAPTER 7**

General Conclusions
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Chapter 7 outlines the whole thesis, including its theoretical, policy, and managerial consequences. Additionally, the chapter discusses the study's limitations, knowledge gaps for further research, and overall conclusions.

## THESIS ABSTRACT

Changes in climate and land-use, collectively called environmental changes, have been a source of concern globally, particularly in dryland grasslands, where people still heavily rely on services from these ecosystems. Extreme climatic conditions have been projected to increase both in intensity and frequency globally. In semi-arid regions, drought is anticipated to occur more frequently and to last longer as a consequence of climate change. Moreover, as human populations continue to grow, there is an increase in demand for natural resources that are already diminishing. Consequently, the combination of these factors has a negative effect on the functions and services of the dryland grassland ecosystems. Therefore, to counteract the degradation of these socio-economically significant ecosystems, it is vital to understand how these systems respond to the long-term effects of drought and grazing.

Limpopo province is largely dominated by drylands; comprising arid, semi-arid and dry sub-humid ecosystems. In Limpopo province, rangelands and agroforestry systems deliver important ecosystem services. Arable lands, rangeland, agroforestry, and orchards are three major land-use types contributing greatly to local livelihoods within Limpopo’s multi-use landscapes. Motivated by the above mentioned factors this study had the following objectives; (i) to review the impact of climate change on dryland grasslands, (ii) to evaluate ecosystem functioning through the assessment of climate-related effects on taxonomic diversity and density demography from the grass layer, (iii) to analyse the effects of drought and grazing on the grass layer and to understand the factors affecting tree populations, particularly tree establishment patterns, (iv) to measure ecosystem service provision from the savanna ecosystem and also, to bridge the knowledge gap on the importance of biodiversity in an ecosystem.

To achieve the aforementioned objectives, a comprehensive literature analysis was conducted on the effects of climate change on dryland grasslands to assess the magnitude of this impact and the existing understanding of vegetation dynamics in the face of climate change. The study also took advantage of the large-scale field experiment which evaluated, through precipitation manipulation, the impact of drought on grazed and ungrazed vegetation in the dryland grasslands of Limpopo province,

South Africa, labeled DroughtAct experiment. In the DroughtAct experiment, passive rain-out shelters and grazing ex-closure fences were set up to simulate a severe drought in combination with differing resting schemes of the rangeland. This was done in order to assess the effect of previous drought events on herbaceous vegetation. Grazing and drought treatments were implemented across four treatment plots per block, via a full factorial design. The study also took advantage of the steep gradient of climatic aridity in Limpopo province and used a space-for-time substitution to evaluate the effects of climate-induced risks and factors impacting the establishment of encroaching woody species under conditions of climate change. Two climate zones and soil types were selected; semi-arid vs. dry sub-humid zone, and Glenrosa soil vs. Hutton soil. Data analysis was executed using the R statistical software package.

The examination of literature revealed that African dryland ecosystems are especially vulnerable to the effects of climate change, resulting in biodiversity loss, structural and functional changes to the ecosystem, and a diminished capacity to deliver ecosystem services. Climate change's most susceptible species and functions have a great potential to be utilized as early warning signs. Furthermore, precipitation manipulation experiments are a great tool for investigating the impact of climate change as they allow for precipitation reduction below the natural range. There is still a general lack of information regarding the effects that extreme climatic conditions have on ecosystems and the mechanisms that determine how ecosystems respond and recover from stress and disturbances.

The DroughtAct experiment showed that prolonged drought had a substantial and negative impact on the biomass output of the vast majority of taxonomic groups and plant functional types (PFTs). This reduction in biomass production from the grass layer results in limited grazing for livestock, which is a primary ecosystem service provided by dryland grasslands. However, the study revealed that few species and PFTs were resistant to the effects of prolonged drought and grazing. In general, the study showed that long-term drought and grazing winners were primarily forbs and narrow-leaved perennial grasses with low leaf area (LA) and high leaf dry matter content (LDMC). Furthermore, the negative impact of drought on the taxonomic richness and species per unit area and ultimately diversity, worsened as the drought period increased. Additionally, grazing exclusion (resting) was shown to have a negative influence on species richness, abundance, and diversity, especially over long periods of time.

Bottom-up mechanisms such as soil type had a greater impact on the establishment, recruitment, and survival of invading woody species than top-down mechanisms such as precipitation. In addition, the significant correlation that was established in the study between the age of trees and the circumferences of their stems, measured at breast height, provided evidence that non-destructive methods of estimating the age of trees are feasible. Further development of non-invasive approaches in the field of dendrochronology is also made possible by these findings.

The findings of this thesis indicate, on the whole, that; to gain a better understanding of dryland vegetation dynamics in the face of drought, researchers need to investigate further the impact of climatic extremes on ecosystem functions and services. Moreover, winners and losers of long-term drought can be distinguished by their unique characteristics; hence, taxonomic groups and functional characteristics could be utilized as early markers of veld degradation, which would permit timely management interventions. The negative impact of long-term drought and grazing on the grass layer limits the ecosystem’s capacity to carry livestock and wildlife for extended periods, thus impacting the livelihoods of the people who rely on these ecosystems. In addition, the tendency of higher tree establishment in lower rainfall years suggests that drought could be a driving factor for woody vegetation propagation.

The trait-based approach is very instructive when it comes to researching the dynamics of vegetation in dryland grasslands. This is especially true when considering the effects of changing climate and land-use. This study has contributed to a better knowledge of the ecosystem function under changing climate and land-use, which is the basis of enhancing the resilience of different land-use systems and reducing risks to ecosystem functions and services while optimizing production.

# CHAPTER 1: GENERAL INTRODUCTION

## 1.1 SAVANNA ECOSYSTEM

Savanna vegetation covers approximately 20% of the world's land surface and accounts for over 30% of global net primary production (Hutley and Setterfield, 2019). Although, the term savanna is a contentious topic, according to Sankaran et al. (2008) savannas are ecosystems that consist of a continuous herbaceous layer and a discontinuous woody stratum. It is, however, noteworthy that the fundamental driver of tree-grass interaction dynamics is the availability of moisture and nutrients (Van Der Waal et al., 2009). Although it is often not considered to be a primary driver, land-use has also been shown to be a major determinant of savanna vegetation structure (Luoga et al., 2004).

Savannas are socio-economically important because, in southern and central Africa, they contain a large and rapidly growing proportion of the world's human population and a majority of its rangelands and livestock (Scholes and Archer, 1997). However, African rangelands are often thought to be undergoing degradation, owing mostly to human population growth and the resultant land-use consequences (Rutherford et al., 2012). In drylands, pasture-based animal production and, to a lesser extent, crop production are the two most common forms of land-uses. Therefore, the stability of people's livelihoods and sources of income in drylands is highly dependent on the revenues generated by crop yields and pasture production (Gillson and Hoffman, 2007).

A degradation of savanna ecosystems typically results in a strong decline in ecosystem services such as recharge of groundwater resources, the protection of soils from erosion or the provision of grass biomass for extensive livestock production, which is the main form of land-use (Sankaran et al., 2005). South African ecosystems have experienced changes in vegetation and a loss of biodiversity in recent decades (Chown, 2010). Moreover, because rapid change has a detrimental effect on ecological function, biodiversity, and the provision of ecosystem services, it is vital to forecast threshold behavior for biodiversity conservation and ecosystem management (Gillson, 2015). The most important drivers governing savanna vegetation are the availability of resources (e.g., water, nutrients) and disturbance regimes (e.g., fire, herbivory) (Sankaran et al., 2008). As a result, for better management of savanna vegetation, particularly in the face of climate change and variability, empirical data on the impacts of drought and grazing on taxonomic and functional diversity is required, which is currently lacking in many natural and agro-ecosystems, notably in Africa.

Many studies have demonstrated that the biodiversity of open woodlands and tropical forests may have a significant impact on the delivery of ecosystem services (ES) (van der Sande et al., 2017). Dominant plant strategies, or the most prevalent functional trait values, have been discovered to be more essential than other biodiversity factors (Conti and Díaz, 2013, van der Sande et al., 2018). Additionally, a recent tropical forest modeling study revealed that the diversity of plant traits has a strikingly beneficial effect on the robustness of ecosystem service provision under climate change conditions (Sakschewski et al., 2016). Thus, it was crucial to consider the significance of functional composition and diversity when investigating the implications of global change on ecosystem service delivery from the savanna ecosystem. Unfortunately, the general understanding of how biodiversity regulates the potentially interacting effects of climate and land-use change on a variety of ecosystem services remains limited.

The study took advantage of the large-scale field experiment Drought Act, which sought to evaluate the impact of extreme drought (66% reduction of ambient rainfall) and moderate grazing on ecosystem function and services. In the Drought Act experiment, passive rain-out shelters and grazing ex-closure fences were set up in the growth period 2014/15 to simulate a severe drought in combination with differing resting schemes of the rangeland. The DroughtAct experiment was conducted in the Limpopo Province of South Africa, which is an appropriate location for drought research because climate change models predict an increased likelihood of drought in this region. The experiment evaluates ecosystem services and functions under drought (D+) and non-drought conditions (D-), from grazed (G+) and ungrazed (G-) vegetation.

## 1.2 THE ROLE OF BIODIVERSITY

African savannas are experiencing a rapid land cover change, which threatens biodiversity and decreases ecosystem productivity and services as a result of habitat and biomass loss (Dimobe et al., 2018). Dominant plant strategies – the most abundant functional trait values – have been found to be even more important than other biodiversity attributes (van der Sande et al., 2018, Conti and Díaz, 2013). Moreover, a recent modelling focusing on tropical forests found that the diversity of plant traits had strikingly positive effects on the resilience of ecosystem services (ES) provision under conditions of climate change (Sakschewski et al., 2016). Hence it was of critical importance to assess the role of functional composition and diversity when studying global change effects on ES delivery from savanna woodlands. Unfortunately, there is still a limited understanding of how biodiversity modulates the potentially interactive effects of climate and land-use change on multiple ESs.

In this context, only six plant traits have been recently found to be sufficient for capturing functional differences in plant growth, survival and reproduction (Díaz et al., 2016). These are leaf dry matter content (LDMC), leaf nutrient content (LNC), leaf toughness measured as tensile strength, leaf area (LA) displayed per unit of C, measured as specific leaf area (SLA), which is calculated as the ratio of leaf area to leaf dry mass (Awal et al., 2004)., plant height and wood-specific gravity, measured as the ratio of the oven-dried mass of a wood sample divided by the mass of water displaced by its green volume (Chave et al., 2005). Furthermore, three major components of plant functional diversity could be put forward as drivers of carbon storage in ecosystems: the most abundant functional trait values, the variety of functional trait values and the abundance of particular species that could have additional effects not incorporated in the first two components (Conti and Díaz, 2013).

Global biodiversity is threatened by several human-induced processes, such as land-use change and invasive species (Trakhtenbrot et al., 2005). Climate change is affecting species distribution and ecosystem services (Lovejoy and Hannah, 2005). Ecological experiments, observations, and theoretical developments show that ecosystem properties depend greatly on biodiversity in terms of the functional characteristics of organisms present in the ecosystem and the distribution and abundance of those organisms over space and time. Hooper et al. (2005) arrived at the following conclusions;

(i) Certain combinations of species are complementary in their patterns of resource use and can increase average rates of productivity and nutrient retention. At the same time, environmental conditions can influence the importance of complementarity in structuring communities. Identification of which and how many species acts in a complementary way in complex communities is just beginning.

(ii) Having a range of species that respond differently to different environmental perturbations can stabilize ecosystem process rates in response to disturbances and variation in abiotic conditions. Using practices that maintain a diversity of organisms of different functional effects and functional response types will help preserve a range of management options.

Susceptibility to invasion by exotic species is strongly influenced by species composition and, under similar environmental conditions, generally decreases with increasing species richness. However, several other factors, such as propagule pressure, disturbance regime, and resource availability also strongly influence invasion success and often override the effects of species richness in comparisons across different sites or ecosystems.

## 1.3 PROBLEM STATEMENT

According to Mucina and Rutherford (2006), the savanna biome is the largest biome in southern Africa, occupying 46% of its area, and over one-third of the area of South Africa. However, Ngaruka (2011) reported that one of the most intractable problems in savanna management is the thickening up or invasion by indigineous woody plants (bush encroachment), which then suppresses the productivity of the grass layer. Any degradation occurring in the savanna ecosystem will have a strong impact on local human populations, especially on rural livestock-dependent communities (Grellier et al., 2013), because this ecosystem is extensive, and socio-economically important as it is responsible for almost 30% of the global net primary production. Furthermore, Giannecchini et al. (2007) reported that rural areas of South Africa are home to approximately 2.4 million rural households, who still depend heavily on the land and its natural resources for their livelihoods.

South Africa has a total land area of 122 Mha subdivided into 6.3 Mha (50%) used for grazing; 1.7 Mha for nature conservation, 0.9 Mha is arable farmland and the remaining area supports forestry, urban and rural communities, mining and other activities (Whitbread et al., 2011). Makhado et al. (2014) reported that the forestry and agricultural sectors are the front runners in terms of vulnerability to the impacts of drought and other forms of climatic variability in southern Africa. This vulnerability to climatic change is detrimental because former Bantu stands or homelands of South Africa are home to a large number of rural households, who still depend heavily on the land and its ecosystem services. Van de Pol and Jordaan (2008) indicated that South African veld is severely degraded, with 60% in a bad, 30% in an intermediate and 10% in a good condition.

Desertification, in the form of reduced perennial vegetation cover, increased bare ground, soil erosion and reduced rain use efficiency, is thought to occur in steps which can be triggered by extreme climatic events such as drought (Vetter, 2009). Liancourt et al. (2005) found that the net outcome of biotic interactions among plants is the sum of co-occurring negative and positive interactions, with facilitation generally increasing in importance with increasing abiotic stress. There is, however, no consensus as to how these drivers interact to influence the structure and function of the savanna (Bond, 2008). African rangelands are commonly perceived as undergoing widespread and serious degradation mainly through human population increase and associated land-use impacts (Rutherford et al., 2012). Land degradation has commonly been defined as land-uses that lead to a persistent loss of ecosystem productivity  (Scholes and Biggs, 2005). Growing human populations, rising food and fuel prices, political changes and uncertainties around land reform add to the challenges of coping with droughts and climate change in South Africa’s arid and semi-arid rangelands (Vetter, 2009).

There is still a limited amount of large-scale research that combines observational and manipulative approaches in assessing land-use, grazing and global change agents in South Africa. This creates a knowledge gap that has negative impacts on the understanding of vegetation dynamics and ultimately, a suitable range of land management strategies. Wessels et al. (2004) indicated that desertification has proved extremely difficult to quantify and the lack of appropriate data is widely regarded as a major obstacle to progress in this field. Furthermore, very little information has been established on the factors, patterns and dynamics of bush encroachment, particularly how drought and land-use in South African savannas are linked to the occurrence of bush encroachment. Generally, factors causing bush encroachment are poorly understood (Ward, 2005).

## 1.4 RATIONALE

Management regimes need to be intensified because the savanna-forest ecosystems exhibit threshold behaviour, which has been described in terms of alternate stable states, where feedbacks between fire and vegetation maintain mutually exclusive assemblages of fire and shade-tolerant plant communities (Gillson, 2015). Increasing levels of savanna degradation result in a strong decline in ecosystem services, which is the main form of land-use (Sankaran et al., 2005).

Communal areas are multiple-use landscapes and are transformed by a range of interacting environmental and human factors (Twine, 2005). In South Africa, communal areas are predominantly engaged in the production of crops and the keeping of livestock. However, few studies have assessed the relationships between land-cover change and socio-economic factors at a local level in the former bantustans of South Africa (also referred to as ‘homelands’) (Giannecchini et al., 2007). Consequently, there is limited knowledge about the impact of climate change and land-use on the ecosystem's multi-functionality.

As climate and land-use change, the management of rangeland and natural resources must also change and adapt. However, lack of knowledge, particularly on a local level, causes mismanagement and degradation of the savanna ecosystem. Precipitation manipulation experiments, which potentially offer great insight into understanding the effects of drought on rangeland, are limited in Africa, particularly in Limpopo province. Therefore, this study sought to bridge the knowledge gap by firstly, assessing global change agents’ direct and indirect biodiversity-mediated effects on ecosystem functions and services, particularly winner and loser species and secondly, evaluating the combined grazing and drought effects, and to further, explore the relative importance of bottom-up mechanisms (competitive release in post-drought years) and top-down mechanisms (severe grazing and drought) for tree establishment and lastly, use a precipitation manipulative approach to examine how vascular plants are distributed in space. This approach provided a basis to not only assess current plant-environment relationships but also to gain insights into the response of grazing lands to future land-use and climatic conditions.

## 1.5 AIMS & OBJECTIVES

The overall aim of this study was to generate data that will provide a better understanding of vegetation dynamics and insight into strategies of range management in the face of changing climate and land-use.

The specific objectives of the study were to:

(i) Evaluate ecosystem functioning through the assessment of climate-related taxonomic diversity and density demography from the grass layer.
(ii) Analyze the effects of drought and grazing on the grass layer and determine the factors affecting tree populations, particularly tree establishment patterns.
(iii) Measure ecosystem service provision from the savanna ecosystem and also, bridge the knowledge gap between local ecological knowledge and scientific research on the importance of biodiversity in an ecosystem.

## 1.6 RESEARCH QUESTIONS AND HYPOTHESES

The following research questions and hypotheses were formulated in an effort to address the problem at hand:

**Question 1:** Which diversity-mediated factors have the greatest influence on ecosystem functions and services?

**Hypothesis 1:** Ecosystem functioning is not determined, to a large extent, by taxonomic diversity and density demography from the grass layer.

**Question 2:** What is the relative importance of bottom-up mechanisms (such as competitive release following drought) and top-down mechanisms (grazing and drought) for the recruitment of an encroacher tree species?

**Hypothesis 2:** Drought and grazing do not affect the grass layer and tree populations, particularly tree establishment patterns.
**Question 3:** What are the direct and indirect effects of changing climate and land-use on multiple ecosystem services delivered by Limpopo's savanna vegetation?

**Hypothesis 3:** There will be a gap between research and local ecological knowledge, leading to mismanagement of natural resources and, ultimately, a disproportionate loss in ecosystem services provided by savanna vegetation.

# CHAPTER 2: LITERATURE REVIEW

## 2.1 EFFECT OF CLIMATE CHANGE ON ECOSYSTEMS

The burning of fossil fuels and the destruction of forests are contributing to an increase in atmospheric concentrations of greenhouse gases that are approaching levels that have not been seen in the last 20 million years (Beerling and Royer, 2011). Consequently, average temperatures and precipitation have been greatly impacted (Meehl et al., 2007), as a result, extreme weather events such as droughts and floods are more likely to occur (Stocker, 2014). Human-caused climate changes have an impact on both natural and man-made systems, and are often described in terms of the global mean temperature (Smith et al., 2009). Species' response to human-induced climatic changes generally varies based on their traits. Therefore, changes in climatic conditions serve as a significant driver of natural selection (Sandel et al., 2011), impacting all aspects of biodiversity. Even though other variables such as local temperatures, seasonal and diurnal temperature patterns, precipitation, and storm tracks are more directly related to climate impacts. Global-mean surface temperatures (GMT) are a useful indicator of the overall scale of anthropogenic climate change over time (Smith et al., 2009).

Climate change has been a contentious issue in ecology for a long period of time, mostly owing to its detrimental effects on ecosystem services and the livelihoods of those who rely significantly on these ecosystems. According to Godde et al. (2019), changes in mean temperature and increased climatic variability are reducing grasslands' carrying capacity, compromising the livelihoods of millions of people and the health of grassland ecosystems. The type, frequency, and intensity of extreme weather events such as drought, heat waves, and flooding are expected to change as the earth's climate changes; wet extremes are expected to become more severe in many areas with expected increases in mean precipitation, while dry extremes are expected to become more severe in areas with expected decreases in mean precipitation (Meehl et al., 2007). As a result, severe events such as drought, flooding and heatwaves are becoming more essential drivers of future ecosystem function and dynamics. Sintayehu (2018) reported that climate change is expected to have a significant negative influence on all levels of biodiversity, and this loss of biodiversity has the potential to alter the structures and functions of African ecological systems.

Climate change has been shown to have a detrimental effect on natural ecosystems, resulting in severe biodiversity loss in African drylands (Bellard et al., 2012). As a consequence, to minimize global biodiversity losses conservationists must identify those species which are most susceptible to the impacts of climate change and further develop management strategies to mitigate those losses (Pacifici et al., 2015). Conservationists and policymakers working in dryland grasslands must be particularly prepared to deal with prolonged periods of severe weather, such as drought (Godde et al., 2019), notably in the context of Africa, which has been considered especially susceptible to the impact of climate change (Sintayehu, 2018). According to Midgley et al. (2002), climate change's most susceptible species could be investigated and utilized as early warning signs, as well as for empirical validation of forecasts.

It is critical to investigate the interactions between biodiversity, ecosystem services, and climate change to develop effective management strategies for dryland grasslands in the face of future climatic extremes. To get accurate estimates of the impacts of climate change on ecosystems, it is necessary to study species-specific responses as well as changing landscapes, variation in local conditions, and species interactions (Ibáñez et al., 2013). There is a scarcity of data on the influence of climate change on many components of African biodiversity, especially their functional or interacting role in ecosystem integrity and stability (Sintayehu, 2018).

## 2.2 THE SAVANNA ECOSYSTEM

### 2.2.1 Characterization of the ecosystem

Savannas are ecosystems in which woody plants are dispersed across a grassland, distinguishing them from grasslands which are devoid of trees and closed forests devoid of dense grass cover (Hutley and Setterfield, 2019). The Savanna biome is distinguished by several major macroclimatic characteristics, including: (1) seasonality of precipitation, which is characterized by the alternation of wet summer and dry winter periods; and (2) a (sub)tropical thermal regime, which does not have or typically has a low incidence of frost (Mucina and Rutherford, 2006). To a large extent, the grass layer is composed of C4-type grasses, which have a competitive edge in environments with warm growth seasons. However, C3-type grasses predominate in areas that get a greater proportion of their rainfall throughout the winter (Cowling et al., 1997).

The height of the shrub-tree layer in bushveld may vary from 1 to 20 meters, however, the average range is between 3 and 7 meters. Furthermore, in areas where grazing is excessive, the shrub-tree component of the vegetation may ultimately come to predominate (Mucina and Rutherford, 2006). The great majority of savanna vegetation types are utilized for grazing, most often by cattle or game; nevertheless, goats are a significant stock species in the southernmost savanna vegetation types (Rutherford and Westfall, 1994).

The most extensive biome in Africa is represented by the savanna vegetation found in South Africa and Eswatini, which together form the greatest southern stretch of this biome (Figure 2.1). It covers 399 600 km$^2$ of South Africa and 74.2 km$^2$ of Eswatini, which is 32.8 percent of South Africa and 74.2 percent of Eswatini, respectively (12 900 km$^2$) (Mucina and Rutherford, 2006). However, the majority of savannas are considered to be tropical, and they take up the vast majority of the area on the continents to the south (Huntley and Walker, 1982), in addition to taking up a portion of the continents to the north in some locations (Mucina and Rutherford, 2006). Rainfall, largely occurring in summer, is one of the most important but also one of the most limiting environmental factors in arid and semi-arid environments since it controls plant productivity (O'Connor et al., 2001) and survival (Snyman, 2004).

Nearly 6 million hectares of communal rangelands in South Africa are home to 2.4 million rural households (Shackleton, 2001). This ecosystem is socio-economically important because an estimated 150 million people living in rural and urban areas of Southern Africa are dependent on the extraction of natural resources from semi-arid savannas to maintain their livelihood (Ryan et al., 2016), Including thatching grass, reeds, poles, and other resources for construction and crafts, as well as food, fresh water, and traditional medicines (Schuyt, 2005). The use of these natural resources and the overall disruption caused by humans have had a considerable influence on the flora found in communal savannas, which has led to shifts in the demographic characteristics of different species (Shackleton, 1993). Because these changes have immediate ramifications for communities who rely on the ecosystem for their means of subsistence, it is crucial to understand both the mechanisms that induce changes in the vegetation of communal rangelands and the effects of those factors.

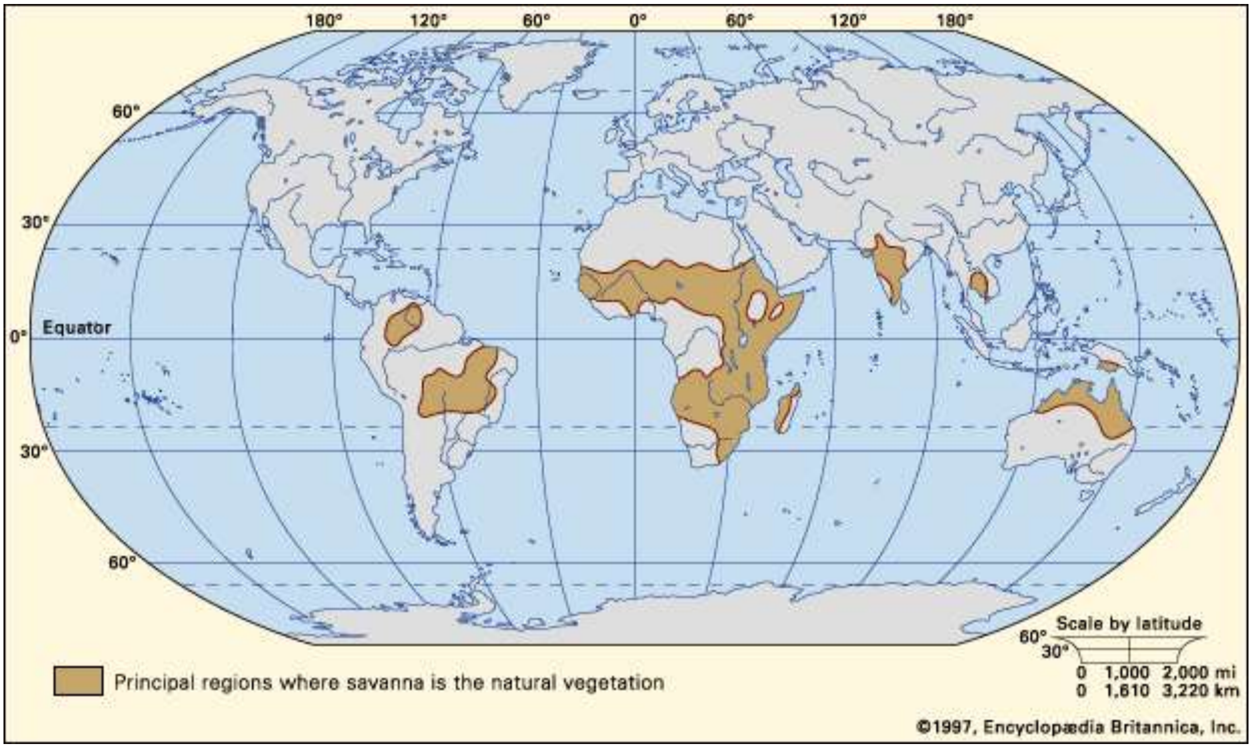


**Figure 2.1** The savanna biome's global distribution, where savanna is the natural vegetation. Adopted from https://thesavannabiomewebsite.weebly.com/

### 2.2.2 Savanna ecosystem degradation

According to Asner et al. (2004), grasslands and savannas cover 51% of the global land surface, and these biomes support around 40% of the world's population (Reynolds et al., 2007). Any degradation in these ecosystems will have a severe impact on the human populations in the region, especially on the rural communities that depend on livestock production (Grellier et al., 2013). Because of its socioeconomic relevance, this ecosystem must be adequately managed and protected for livestock production to be viable and continuous. This is critical for guaranteeing farmers' financial stability and the general health of the economy. However, according to UNCCD (1994), around 10 to 20% of this ecosystem is severely degraded, and moreover, as a result of changing climate and population expansion, it is anticipated that this degradation will extend significantly in the coming years (Reynolds et al., 2007).

Since over one hundred years ago, the phenomenon known as "bush encroachment" has been recognized as a problem for rangelands in southern Africa (O’Connor and Page, 2014). It is characterized as an increase in the abundance of woody vegetation in grassland and savanna biomes (Turpie et al., 2017). The subsequent recognition of bush encroachment for several savanna vegetation types throughout the first half of the twentieth century led to its emergence as one of the top three perceived rangeland concerns across 25 percent of South Africa's magisterial districts in recent years (Hoffman et al., 1999). Research conducted by Reed et al. (2015) discovered that land degradation caused by bush encroachment has a negative impact on ecosystem services provided to the surrounding community, which frequently results in socio-economic challenges such as a loss of income and insufficient production to support livestock keeping.

Changes in fire regimes, the amount of pressure exerted by cattle grazing, and the change in climate are the three components that are conventionally considered to be the causes of this dynamic in both North America and Australia (O’Connor and Page, 2014). According to (Ward, 2005), who holds an opposing position, suggests that the conventional knowledge of the causes of bush encroachment is limited, and rainfall amount and frequency, as well as certain soil nutrient levels, may be key drivers of this phenomenon. Colonialism and subsequent political events, which resulted in a system of land ownership and consequently land-use that is not prevalent in other regions afflicted by bush encroachment, are driving local bush encroachment in South Africa (O’Connor and Page, 2014). Due to the unique sources of bush encroachment in South Africa, there is a scientific rationale for examining this phenomenon locally in order to add to the body of knowledge that guides the understanding and, ultimately, management of bush aggregation.

It is well known that the presence of invasive alien plant species and the expansion of bush encroachment may impact the function of an ecosystem, diminishing the potential to deliver a variety of ecosystem services essential for economic growth and sustainable development (Favretto et al., 2016). Encroaching woody species comprise both indigenous and exotic woody species, resulting in two types of bush encroachment: (a) the expansion of indigenous woody plant species and (b) the invasion of exotic/alien woody species in savanna and grassland environments (Mucina and Rutherford, 2006). The species responsible for the majority of bush encroachment and invasion in southern Africa, according to extension officers, are six legumes: *Vachellia hebaclada, V. karroo, V. nilotica, V. tortilis, Senegalia mellifera,* and *Dichrostachys cinerea*, as well as *Rhigozum trichotomum* and *Tarchonanthus camphoratus* in the Northern Cape, South Africa (Hoffman et al., 1999). Consequently, a complete study of any one of the six key encroachers may provide a better understanding of the encroachment drivers, which is crucial for the management of bush encroachment.

### 2.2.3 The effect of land-use change on the function of the savanna ecosystem

More than half of the earth's land surface is covered by drylands, which are comprised of arid, semiarid, and dry sub-humid ecosystems combined (Asner and Heidebrecht, 2005). Asner et al. (2004) reported that drylands are home to 78% of the world's grazing animals, making managed grazing the most common type of land-use worldwide. Despite having a low population density (about 25 people per square kilometer), the African savanna, which is the largest savanna in the world, is rapidly developing (Mauda et al., 2018). Africa has the fastest population growth (Haberl et al., 2005). According to Gerland et al. (2014), Africa's population is estimated to quadruple by 2100, resulting in a significant intensification of the agricultural sector, which will have a severe influence on the savanna ecosystem.

Human activities related to the expansion and intensification of agricultural landscapes for the production of food and biofuels have damaged many of the planet's ecosystems (Barnes et al., 2014). When it was first mapped, the area covered 13.5 million km$^2$, but by the year 2000, 22% of that had been lost and since then, another 50% has been converted to new cropland and settlements (Mauda et al., 2017). The conversion of natural ecosystems to agricultural land-use, together with the associated intensification of that use, has resulted in substantial decreases in biodiversity and the range of ecosystem services (Gibbs et al., 2010). This negatively impacts the livelihood of those communities who rely on these ecosystems (Díaz et al., 2006). One of the most important global environmental problems of today has been land degradation (Reynolds and Stafford Smith, 2002). In drylands, land-use practices such as grazing can change the properties of the vegetation, the quantity of accessible water, the rate of soil erosion and soil compaction, the carbon cycle, and several other ecological processes (Asner and Heidebrecht, 2005).

As urban environments continue to expand, it is becoming increasingly evident that large conservation efforts are required in urban and urbanizing areas to sustainably preserve the threatened biological diversity (Seabloom et al., 2002, Sol et al., 2017). However, in the African context, there’s still limited research effort dedicated in this direction. Furthermore, accurate estimates of the consequences of habitat change on species distributions are necessary for the development of effective policies for the conservation of global biodiversity (Pearson et al., 1999, Mantyka-Pringle et al., 2015). It has been demonstrated that human modification of ecosystems is beneficial to a small number of widely distributed species but detrimental to a large number of species with restricted distribution (Schwartz et al., 2006). Because savanna ecosystems provide essential ecosystem services, it is important to research the impact of land-use change on ecological processes.

It is generally established that changes in land-use, in conjunction with climate changes, have significant detrimental effects on both functional diversity (Flynn et al., 2009) and overall biodiversity. However, the effects of changes in land-use on ecological processes and biodiversity are under-researched and only partially understood (Foley et al., 2011, Flynn et al., 2009). Therefore, it is of the utmost importance that researchers, particularly in Africa, carry out studies that will contribute to and add value to the existing body of knowledge regarding the impact that changes in land-use have on ecosystems and the consequences that these changes have for the livelihoods of people who still heavily rely on ecosystems. To accurately estimate how intensification of land-use may affect ecosystem services, one must be able to analyze biological diversity pertinent to ecosystem function in a reliable manner (Flynn et al., 2009).

### 2.2.4 Measuring productivity in the savanna ecosystem: Abovegroung Net Primary Production (ANPP)

Aboveground net primary production, commonly known as ANPP, is an essential component of ecosystems and is of fundamental importance for practically all matter and energy fluxes in terrestrial ecosystems (Ruppert and Linstädter, 2014). ANPP can be defined as the sum of produced aboveground plant tissue within one year, usually expressed in g $m^{-2}$ or kg $ha^{-1}$ of dry mass (Scurlock et al., 2002). ANPP is not a distinct physical quantity or trait, therefore, it can only be inferred and not measured directly. This is due to the fact that it is a concept rather than a specific metric (Lauenroth et al., 2006). To calculate ANPP, therefore, 1.44 $m^2$ Short-Term Ex-closure (STE) cages are placed in an experimental unit to exclude grazing throughout the growth season. At the end of the growth season, the biomass in the STEs is cut within a $1m^2$ quadrat, oven-dried and weighed. The total dry mass is then extrapolated, using the total area of the experimental unit, to infer how much biomass the area produced in that growth season.

In drylands contexts, the peak standing biomass technique has proven to yield reliable and relevant estimates of ANPP (Scurlock et al., 2002), provided that it is applied correctly (Ruppert and Linstädter, 2014). Therefore, this method was used to calculate ANPP in the DroughtAct Experiment. The peak standing biomass approach relies on a single measurement (or estimate) of biomass taken at the moment when the greatest amount of biomass is present in relation to the unit area (for example, g $m^{-2}$): Peak biomass season. Peak growth, defined as the period of greatest biomass productivity, should not be confused with peak biomass season or short; peak season. At the University of Limpopo's Syferkuil Farm, peak growth can be anticipated during the primary summer months (December, January, and February), and peak biomass can be anticipated later in the season when the length of the season affords the most potential for biomass to accumulate (mid-March to the end of April).

As a result of ANPP being defined as the sum of assimilation minus respiration during a single growing season, the applied surrogate measurement of biomass cannot be confounded by any tissue losses, such as those caused by grazing, fire, or plant pests. Furthermore, the material carried over from the previous season must be eliminated or adjusted for in the surrogate biomass sample. The first type of error (tissue loss), which will result in an underestimating of ANPP, and the second type of error (addition of dead material), which will result in an overestimation, must both be ruled out. Tissue loss will result in an understatement, whereas the addition of decomposing matter will result in an overestimation.

### 2.2.5 Local ecological knowledge and scientific research

Local ecological knowledge (LEK) is a cumulative body of knowledge, practice, and belief, evolving by adaptive processes and handed down through generations by cultural transmission, about the relationship of living beings (including humans) with one another and with their environment' (Berkes, 1993). It is becoming increasingly accepted that in order to achieve sustainability in modern land-use, natural resource management, and conservation efforts, it is necessary to acknowledge the different parties involved, as well as the knowledge and values that they hold (Angelstam et al., 2017, Rutina et al., 2017, Williams et al., 2020). However, scientists and laypeople comprehend ecosystem services in vastly different ways (Murata et al., 2019).

Africa has a high level of biodiversity, accounting for one-fifth of all plant, animal, and bird species on the planet (Siegfried, 1989). African ecosystems are socioeconomically significant because they provide provisioning, support, and regulating ecosystem services that sustain the livelihoods of millions of communities that depend on them, such as food, grazing, browsing, fuel, as well as water purification, erosion and flood control, climate regulation, soil formation, nutrient cycling, etc. (MEA, 2005). Climate change impacts may be detected on a biome, ecosystem, population, community, species and individual scales (Bellard et al., 2012). Furthermore, biota may adapt to climate change in a variety of ways, including physiological changes, productivity, and growth patterns (Cannell et al., 1998). Bellard et al. (2012) discovered, for example, that the capacity of an ecosystem to regulate climate is highly reliant on the variety of species contained in that ecosystem.

The term "ecosystem services" was coined to emphasize and clarify the extent to which the well-being of humans and the communities in which they live is dependent on the presence of a functioning ecosystem (Schröter et al., 2014). Due to the fact that the vast majority of ecosystem services may be found in rural areas, especially in South Africa and nations where the majority of the population resides in third-world countries, these communities are vital to the study of ecosystem services (Leemans and De Groot, 2003). However, since the 1980s, the expansion of the literature on ecosystem services has been predominantly driven by scientific discussions, the conclusions of which are used to guide intervention initiatives. In scientific debates, however, knowledge of the rural people whose landscapes the programs are executed is rarely a matter of discussion (Murata et al., 2019). Therefore, developmental programs rarely succeed, and this is mostly due to misperceptions among development actors regarding management interventions, methodologies, and pastoral life (Catley et al., 2013).

Climate change has had a devastating effect on essential ecosystem services, natural resources, and people's livelihoods, putting them all at risk. Fraser et al. (2006) reported that both local ecological knowledge and scientific research contribute to the knowledge foundation that is necessary to promote sustainability and successful biodiversity conservation strategy. Local ecological knowledge (LEK) can shed insight on ecosystem change, especially in under-researched areas such as South Africa's communal rangelands. A study by (Chalmers and Fabricius, 2007) reported that ecological knowledge is unevenly spread, and was held mainly by individual experts rather than groups. Furthermore, the understanding of LEK experts was found to not only be remarkably consistent with that of scientists, but added considerable value to the scientific understanding of the ultimate causes of land-cover changes in the area. However, Tefera and Kwaza (2019) found complementarity and certain discrepancies between LEK and scientific knowledge that need to be ratified. The lack of detailed knowledge from respondents suggests that LEK is eroding in the local communities, necessitating additional training for farmers to expand their management capacity.

The Convention on Biological Diversity (CBD) defines 'biodiversity loss' as a long-term quantitative or qualitative decline in biodiversity components as well as their capacity to supply goods and services, which may be quantified at regional, national, and global scales (STOCK, 1992). Climate change may influence biodiversity in several ways, but at the most basic level, it can reduce genetic diversity in populations via rapid species migration and directional selection, which has the potential to significantly affect ecosystem functioning and resilience (Meyers and Bull, 2002, Sintayehu, 2018). Most research, however, has focused on higher levels of biodiversity, such as community responses, generally disregarding the consequences of climate change on genetic and functional diversity, especially in the African context. As a result, there is an urgent need in the disciplines of protected area management, ecology, and conservation biology to generate predictions of how global environmental change will affect species abundance and distribution.

Changes in climate and land-use have a significant negative influence on the ecosystems of Africa's rangelands, which in turn affects livestock productivity and the way of life of individuals who depend on these ecosystem services for a living. To establish a feeding and grazing strategy that is resilient and adaptable to various environmental changes, it is necessary to take an "all-inclusive" approach, requiring the improvement of local ecological knowledge and the participation of community area residents in any intervention and development programs (Tefera and Kwaza, 2019). To ensure the active engagement of pastoralists, the focus should be shifted from external stakeholders to local pastoralists (Catley et al., 2013), with future management and policy planning for communal rangelands embracing local ecological knowledge (Rutina et al., 2017).

Variability and change are important aspects of all ecosystems (Jones et al., 2017). However, recent changes have resulted in negative impacts on the functionality and stability of many ecosystems. Therefore, the causes of variability, such as climate change, are becoming increasingly central topics in ecological discussions and how communities respond to these variabilities over time. Because of the continually changing climate, species may no longer be suited to the general environmental conditions of a given location, necessitating an adaptation strategy to the new climatic parameters or they may be replaced by species which more adapted to the environmental conditions. To ensure improved biodiversity conservation strategies, further research between LEK and scientific knowledge has great potential to both expand the ecosystem service knowledge and attract stakeholder cooperation in intervention programs (Murata et al., 2019). Therefore, the integration of LEK into contemporary science would provide development organizations with the essential understanding of pastoral systems as well as a foundation for the formulation of planning and policy initiatives (Samuels et al., 2018), thus bridging the knowledge gap between science and LEK.

The directional shift in composition in some communities had little effect on species richness, owing to the observed change in composition being mostly reordering of species abundances rather than the turnover in species composition (Jones et al., 2017). Although there has been significant species loss as a result of climate change, Hoekstra et al. (2005) contend that this is only the tip of the iceberg, and that these extinctions are a symptom of a much larger problem, a global scale 'biome crisis,' which necessitates that the scope of global conservation emphasizes the protection of entire at-risk ecosystems, rather than focusing on 'hotspots' of species diversity. Williams et al. (2020) discovered through a review of the literature that although there are case studies that recognize the significance of multi-stakeholder collaborations in local landscape research, more research is required to explore ways to more effectively link LEK and scientific knowledge in landscape studies, especially in the co-management of these social-ecological systems.

Partnering with local institutions and research centers as well as participatory research methods will promote effective knowledge exchange between scientific communities and stakeholders, thereby enhancing the relevance and impact of interdisciplinary research by aligning it with local capacity building and support through research activities (Born et al., 2009). On the other hand, there is a lack of communication or information sharing between scientists and those in decision-making positions in South Africa (Shackleton et al., 2009). The gap between LEK and scientific knowledge has great capacity to be narrowed. To accomplish this, however, multidisciplinary approaches must be well-coordinated and utilized.

### 2.2.6 Climate extremes: Drought

It is anticipated that the frequency, as well as the severity of climatic extremes, would rise as a consequence of global climate change, and there is an urgent necessity to understand the ecological implications of these changes (Smith, 2011). The severity and frequency of climate extremes, such as drought, heat waves, and periods of heavy rainfall, are expressions of climate change, as has been proven by a prior study (Meehl et al., 2007). There is, therefore, an urgent need to study the relationship between ecosystem function and climatic extremes. Beierkuhnlein et al. (2011) found that extreme weather conditions have the potential to have significant and far-reaching effects on all levels of the ecological hierarchy, from individual organisms to entire ecosystems. Moreover, it is anticipated that these climate extremes will have disproportionately negative effects on plants and ecosystems, and these impacts could contribute to the surpassing of thresholds (Knapp and Fernandez-Gimenez, 2008, Jentsch et al., 2011, Smith, 2011). As a result, forecasting the effects of climatic extremes on species, functional groups, and ecosystems has become crucial to research.

According to some studies, climatic extremes such as extended periods of severe drought have the potential to negatively impact the functioning and stability of ecosystems (Jentsch et al., 2011, White et al., 2021, Dodd et al., 2021). However, according to the findings of the vast majority of research, changes in seasonal timing and the elongation of the intervals between rainfalls may have a higher influence on above-ground net primary production than periods of drought (Knapp et al., 2007, Yang et al., 2008, Heisler-White et al., 2009). Nonetheless, there is still a dearth of information on the relationship between drought and ecosystem function. The impact of changes in climatic factors on ecological processes and ecosystems has been the subject of a multitude of studies. However, research on climate extremes is much less prevalent and is just now emerging as a unique research field in ecology (Jentsch et al., 2011). In Africa, which is considered to be more susceptible to the effects of climate change (Sintayehu, 2018), research focused on the effects of climate change, particularly the effects of the associated climate extremes, should be given a high priority.

Many grasslands are found in seasonal water-constrained locations, and their biomass and composition are particularly sensitive to water supply fluctuations (Knapp et al., 2002). In general, the relationship between water scarcity and productivity can be studied in two ways: (a) spatially, comparing differences in productivity between two sites along a precipitation gradient, or (b) temporally, comparing changes in productivity from year to year in precipitation that occurs within sites. However, while substantial information can be derived from these methodologies, both are limited for prediction purposes because they are observational in nature and the important drivers cannot be manipulated, only measured. Precipitation-reduction experiments are specifically designed to provide information that cannot be found in the two preceding approaches, spatial and temporal, and are thus complementary because they allow for precipitation reduction below the natural range and are thus particularly suited to examine the potential effects of climate drying.

When water is scarce, plant development is frequently stunted, resulting in a decline in the productivity of terrestrial ecosystems on a broader scale, which may result in a loss in net primary production throughout large parts of the earth (NPP) (Estiarte et al., 2016). Munson et al. (2016) found that previously documented declines from a perennial plant cover to an entire desert can be extrapolated, and demonstrated that prolonged water shortages coupled with land-use intensification result in recognizable patterns of vegetation change in dryland regions. Prolonged drought is, therefore, a great threat to the functionality of dryland grassland ecosystems, because perennial vegetation, which is particularly susceptible to water scarcity, is significant because it acts as a primary carbon sequester, the foundation of food webs and wildlife habitat, contributes to soil erosion reduction, and positively influences nutrient cycling (Munson et al., 2011). The growth and establishment of dryland plants are often slow, and hence, the negative effects of climate and land-use changes on vegetation can have far-reaching impacts on dryland vegetation (Cody, 2000).

The evaluation of the ecological effects of climate extremes and the mechanisms that control ecosystem response and recovery remains one of the most difficult issues facing current ecology (Smith, 2011). The majority of the current knowledge of the biological effects of climate extremes is derived from investigations of naturally occurring events (Hoover et al., 2014). However, observational studies have limitations in that specific climate drivers cannot be clearly linked to ecosystem response and recovery (Smith, 2011). Since climatic factors may be directly attributed to ecological responses, experimental methodologies are more suited to studying climate extremes (Reyer et al., 2013). Therefore, experiments investigating precipitation reduction, extreme temperatures, and floods are extremely useful for projecting what will happen to natural ecosystems in the future under various scenarios that involve changing climatic conditions.

# CHAPTER 3: RESEARCH METHODOLOGY–THE DROUGHTACT EXPERIMENT

### 3.1.1 Study region

The investigated dryland grassland is found on the experimental farm of the University of Limpopo (23°.8410’ S; 29°.6950’ E), located in the Limpopo Province, South Africa (Figure 3.1). Limpopo Province is located in a dry savanna sub-region and is South Africa's most northern province. This sub-region is characterized by open grasslands with scattered trees and shrubs (Whitbread et al., 2011). The climate is characterized as semi-arid steppe, with summers that are warm to hot and winters that are moderate. The long-term average temperatures (1994 – 2020) in the winter range from 4.7 degrees Celsius to 19.6 degrees Celsius, with summertime highs of 28.1 degrees Celsius and lows of 17 degrees Celsius on average (Syferkuil Weather Station 2020). The hot, dry areas have an average annual precipitation of 200 millimeters, while the high rainfall zones have an average annual precipitation of 1500 millimeters (Moshia et al., 2008), with most of it occurring between October and April, which is the usual growing season. Both trees and grasses have developed adaptations to cope with the cyclical nature of rainfall, with the grasses going dormant during the dry season and the trees shedding their leaves. (February et al., 2013). The implementation of the study coincided with one of the strongest El Niño events in southern Africa during the past several decades (Organization, 2017), with protracted droughts in numerous South African provinces, including Limpopo Province, making the study region suitable for drought research.

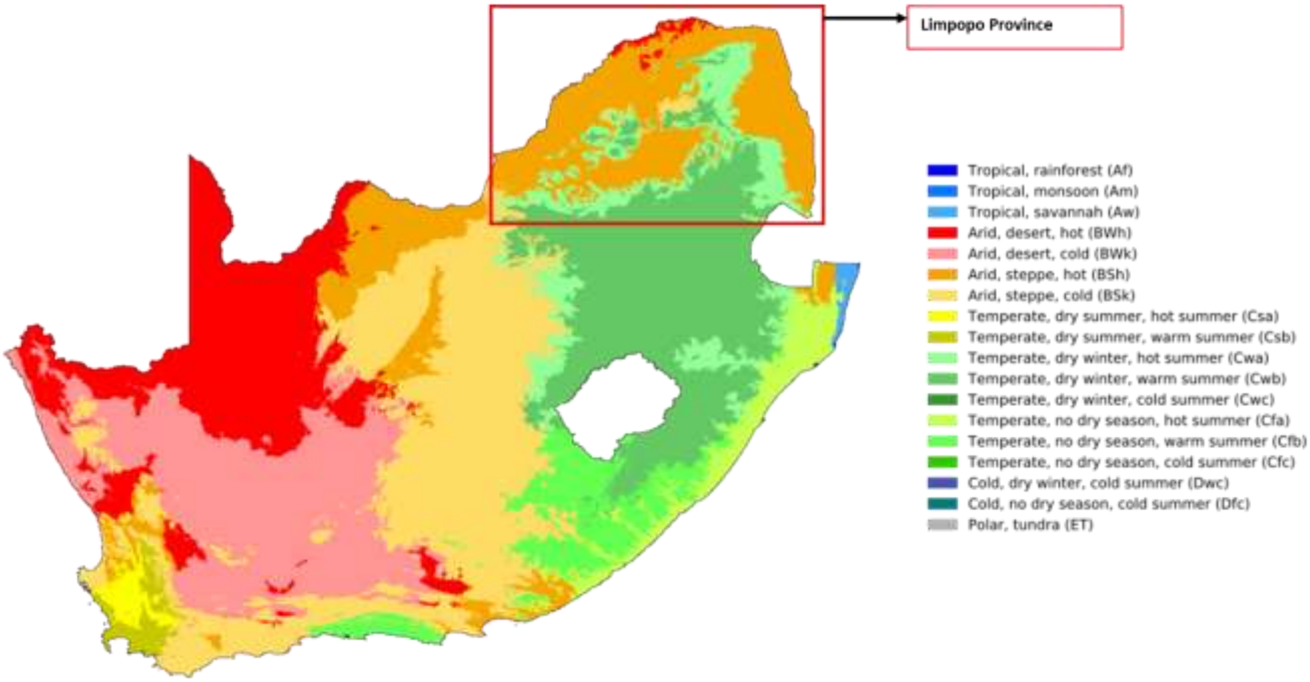


**Figure 3.1** Koppen-Geiger climate classification map of South Africa (1980 – 2016) – from Beck et al. (2018)

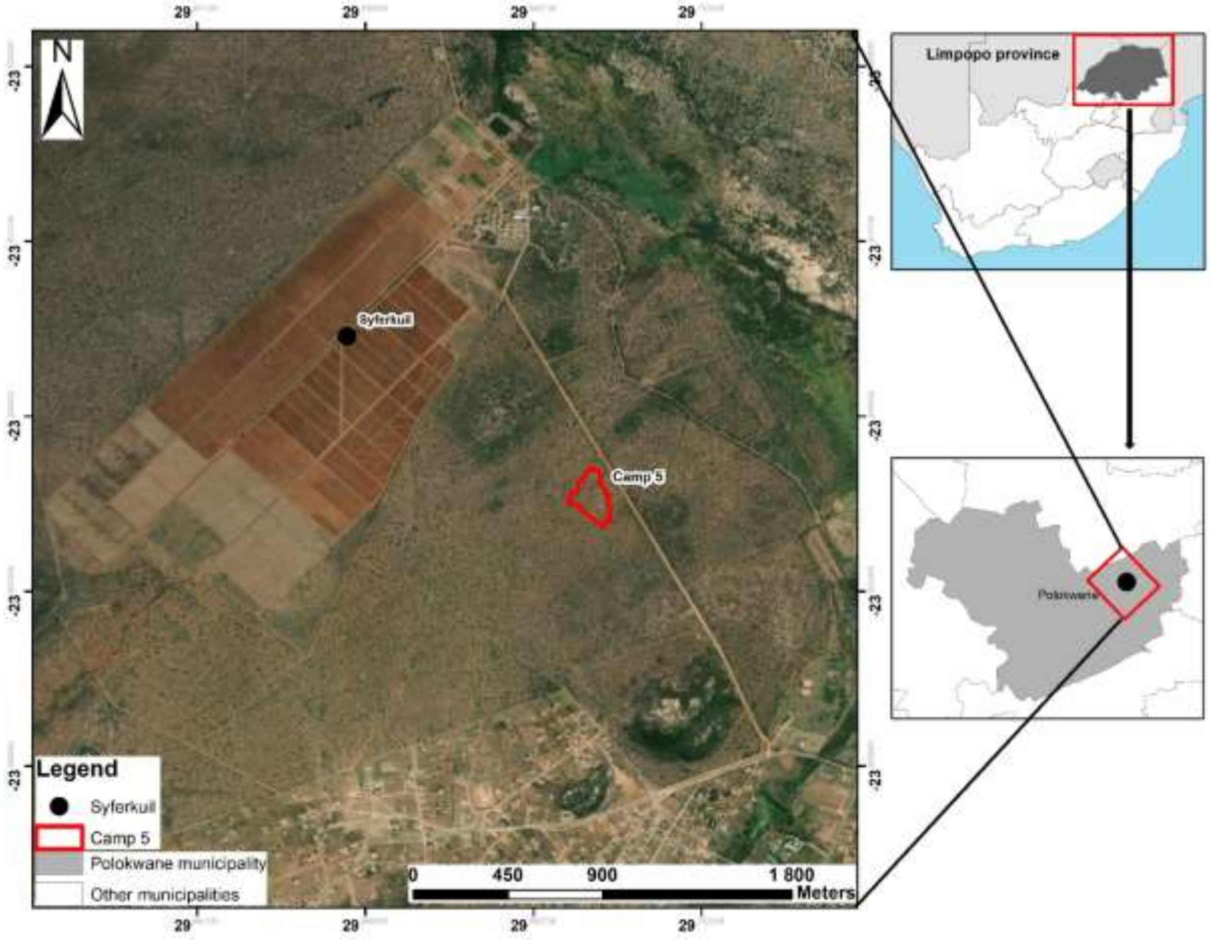


**Figure 3.2** This figure outlines the map of the University of Limpopo's Syferkuil experimental farm within the Polokwane municipality, South Africa.

### 3.1.2 DroughtAct Experiment: Set-up and ecology

#### *3.1.2.1 Ecology*

The experimental site is located on the Pietersburg Plateau False Grassveld (Acocks, 1998). The woody component is dominated by *Vachellia* species such as *Vachellia hebeclada* and *Vachellia tortillis*, whereas the dominating grasses are perennial C4 grasses such as *Digitaria eriantha*, *Heteropogon contortus*, and *Themeda triandra*. Both Glenrosa and Hutton varieties of soil can be found in this region (Group and Macvicar, 1991). During the study years, 2013 to 2020, the experimental camp consisted of 40 hectares (ha) and was a component of a rotational camp system consisting of six camps, which had a total of 280 hectares (ha), all under moderate grazing. Throughout the entirety of the study, a stocking rate of 9 ha LSU-1 was maintained, with an LSU being equal to the weight of a mature cow weighing 450 kg (Meissner, 1983). Under the stated management, grazing duration of 25 to 30 animal herds did not exceed 30 days, with periodic recuperation of at least six or eight weeks throughout the growing and dry seasons, respectively. Grazing management had been implemented six years prior to the trial period, resulting in good veld condition at the commencement of the experiment.

### *3.1.2.2 Treatments*

Experimental blocks and plots were demarcated in December 2013. To test for selection bias, experimental blocks and plots were kept under routine moderate grazing management before treatment deployment. Four blocks (40 x 40 m) were demarcated, with a minimum distance of 40 m between blocks, and were arranged along a grazing gradient away from a watering point with block A closest (~30 m) whereas blocks C and D were furthest (~150 m) from the watering point. Each block was divided into nine 10 x 10 m plots organized in a three by three grid (with 5 m corridors between plots).

At the end of the dry season in October 2014, experimental treatments were introduced. To account for any geographical heterogeneity a completely randomized factorial block design (Figure 3.2) was used. Treatment of grazing (G) had two levels: grazing (**G+**) vs. rest (**G-**) ~ grazing exclusion. Similarly, drought treatment had two levels: Ambient rainfall (**D-**) vs. Drought (**D+**) ~ 66% rainfall reduction. The four treatments were integrated and replicated in each block. Therefore, the following combinations were established: Resting treatment; 1. Grazing exclusion under ambient rainfall conditions (**D-G-**), and 2. Grazing exclusion under simulated drought conditions (**D+G-**). Drought treatment; 3. Grazing under drought conditions (**D+G+**), and 4. Grazing under ambient rainfall conditions (**D-G+**: control) (Figure 3.2).

Four pseudo replicates were implemented at the start of the experiment. The in-block (pseudo-) duplicates, on the other hand, were not intended to be totally independent replicates, but rather stand-alone plots that would undergo a treatment change during the experiment, simulating potential management strategies. By using this methodology, a total of 32 plots (n = 32) were compiled, which consisted of four blocks with four treatment combinations that were repeated twice within each block throughout the course of two years (2014/15 to 2015/16). However, in order to evaluate different land-use scenarios, treatment adjustments on the in-block duplicates were first implemented in the 2016/17 season, resulting in four post-drought/grazing treatments; post-drought and continued resting (**D+$^{p}$ G-**), post drought and post grazing (**D+$^{p}$G+$^{p}$**), post drought and continued grazing (**D+$^{p}$ G+**), continued ambient conditions and post grazing (**D- G+$^{p}$**), resulting in a total of eight treatments per block (Figure 3.2).

The second treatment adjustment was implemented in the 2017/18 season, post drought and post grazing treatment (**D+$^{p}$G+$^{p}$**) and continued ambient conditions and post grazing treatment (**D- G+$^{p}$**) were given up. Therefore, this resulted in four blocks with a total of six treatment combinations for three seasons (2017/18 to 2019/20), making a total of 24 plots (n = 24).

### 3.1.3 Drought simulation: Rainout shelters and trenches

Design that is fixed to simulate drought, passive rain-out shelters (36 $m^2$) were built according to the design described by (Yahdjian and Sala, 2002). On the other hand, both the size and the height of the shelters were adjusted in order to make it possible for the cattle to move and graze without any restrictions. The construction is elevated 3 meters above the ground on the upward slope and 2 meters above the ground on the downward slope. The roof of the structure is made up of bands of polycarbonate (PC) translucent plastic sheets (Figure 3.3). On the downslope-facing side of the shelters, gutters and downpipes were installed to divert water away from the drought plot and the adjacent plots. The shelters were designed using the IDE technique to limit ambient precipitation by 66%, simulating a centennial-scale drought at the study site. Given the site's rainfall history, this is a drought with a 1% chance of occurrence. Moreover, to verify that the design of the rainout shelter does not deviate from the natural environment, biophysical site factors such as light transmittance were monitored, and further measurements were undertaken to analyze the shelter's impact on the microhabitat (Mudongo et al., in prep.).

Trenches were dug around the perimeter of the shelter to the maximum soil depth (up to 70 centimeters) and then an impermeable plastic membrane was installed to protect the drought plots from the lateral flow of soil water. The subplots were created to be smaller than the rain-out shelters, which measured 4.8 meters by 4.8 meters. This constructed a

60-centimeter buffer zone between the plot's boundary and the shelter, allowing edge effects to be mitigated. Moreover, following the strategy by Carlyle et al. (2014), the shelters were designed to obstruct rain from the dominant wind direction.

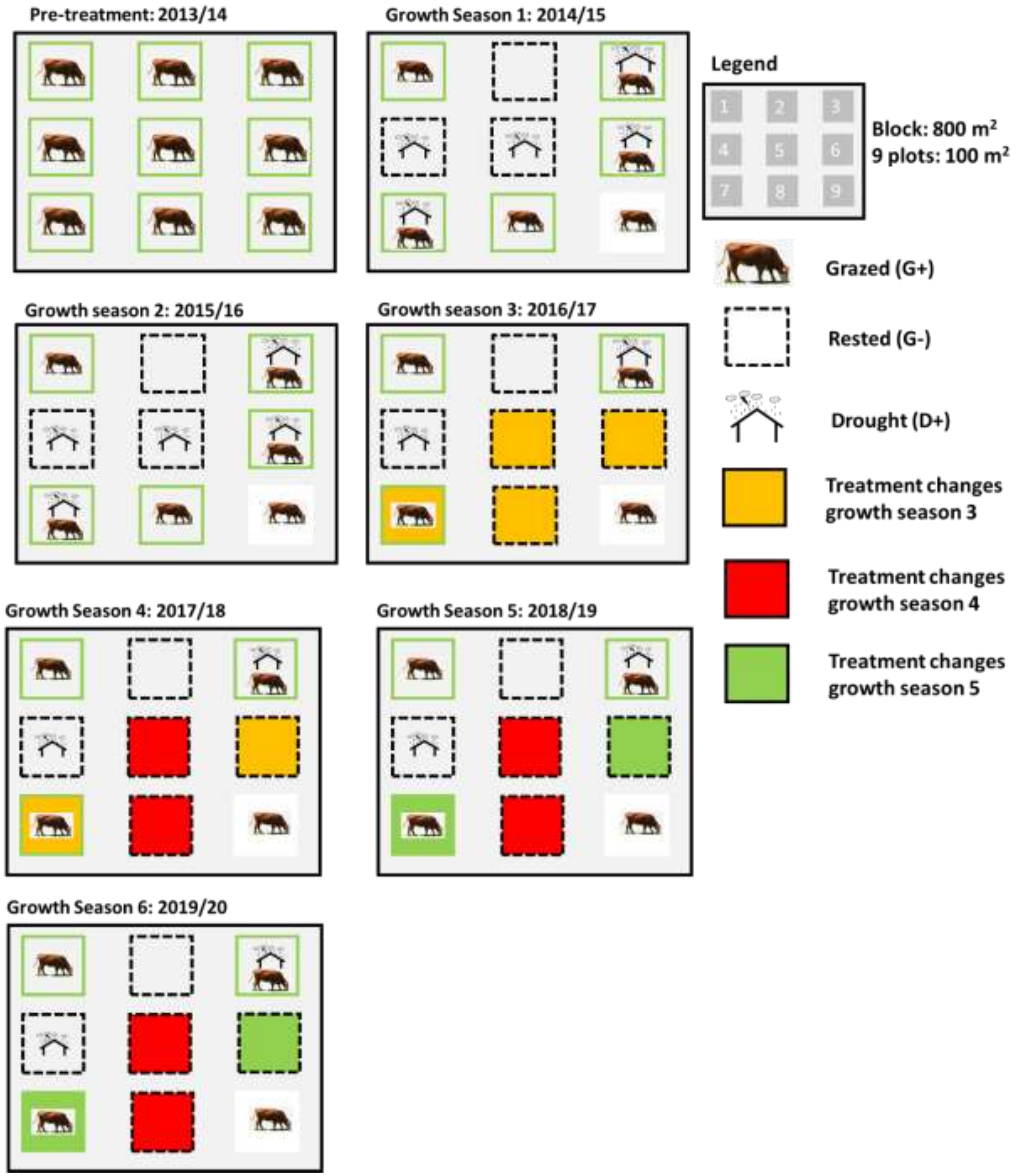


**Figure 3.3** The DroughtAct experimental set-up; showing a grazed pre-treatment year, two years of unchanged treatments of grazing (G+), resting (G-), drought (D+), ambient (D-)

replicated in four blocks with eight plots each, and a third year of treatment changes for drought resistance and resilience evaluation. Drought was removed (drought history), fences were erected (grazing history) and two plots were fertilized using Urea 46 as N fertilizer applied three times during the growing season, as part of the treatment modifications. During the treatment years, the ninth plot was not used modified after Mudongo et al. (in prep.).

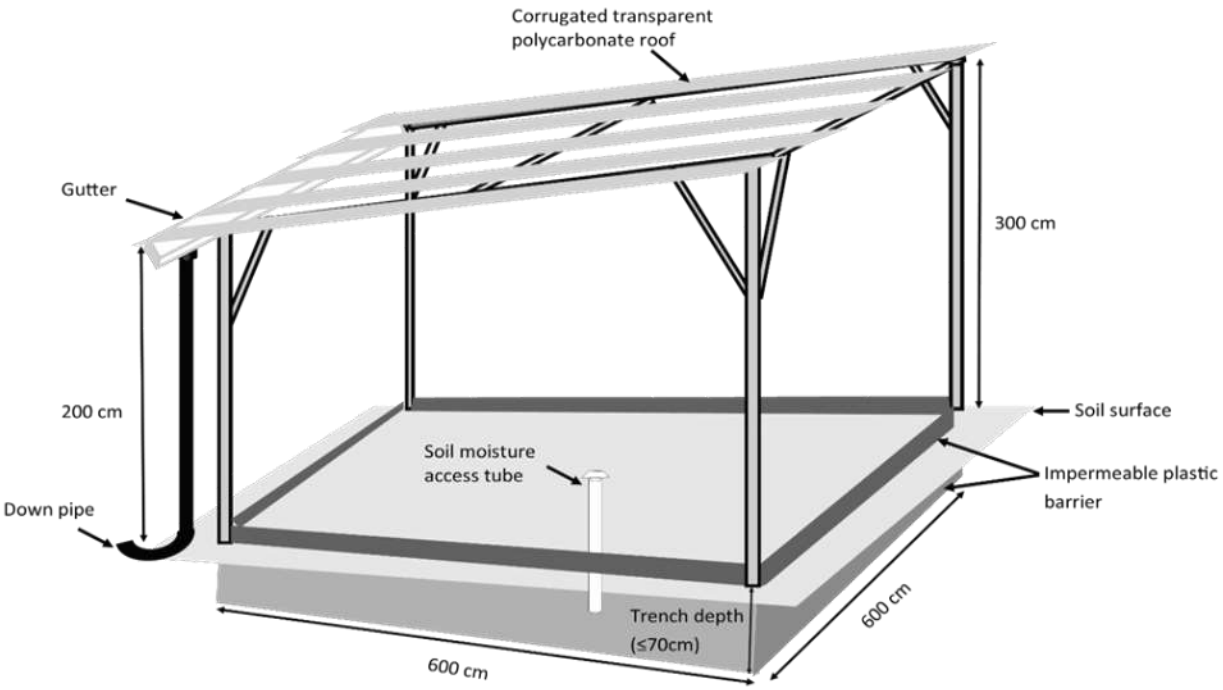


**Figure 3.4** DroughtAct experiment rain-out shelter design – from (Mudongo et al., in prep.).

### 3.1.4 Grazing treatment

Each block contained three 10-meter-by-10-meter long-term exclosure (LTE) plots that were gated with five strands of high tension wire to prevent livestock from grazing there. One plot was established under normal conditions, while the other two were built in drought conditions. Exclosures were created following the 2013/2014 dry season (September/October 2014), and three permanent 1 $m^2$ quadrats were defined inside the subplot for vegetation assessments. The remaining five plots were kept open for cattle grazing, with three under simulated drought circumstances and two under ambient rainfall conditions.

All plots had three paired quadrats, where each pair composed of an area of 1 $m^2$ under 1.2 × 1.2 m movable short term grazing exclosure (STE) cage and a permanent 1 $m^2$ grazed (GRA) quadrat (Figure 3.4). Steel pegs were driven into the ground to secure the STE cages. Before the installation of cages, the peak standing crop system required that all biomass that lay beneath the STEs be cut down to a height of five centimeters (Scurlock et al., 2002, Ruppert and Linstädter, 2014), which achieves uniform starting points by removing residual biomass and carryover material from the previous growing season. For the purpose of determining grazing offtake, the paired quadrat design was utilized (calculated as the difference between standing biomass between STE and GRA). Although the GRA was continuously grazed throughout the study period, the STE was moved around the GRA plot each season to avoid bias.

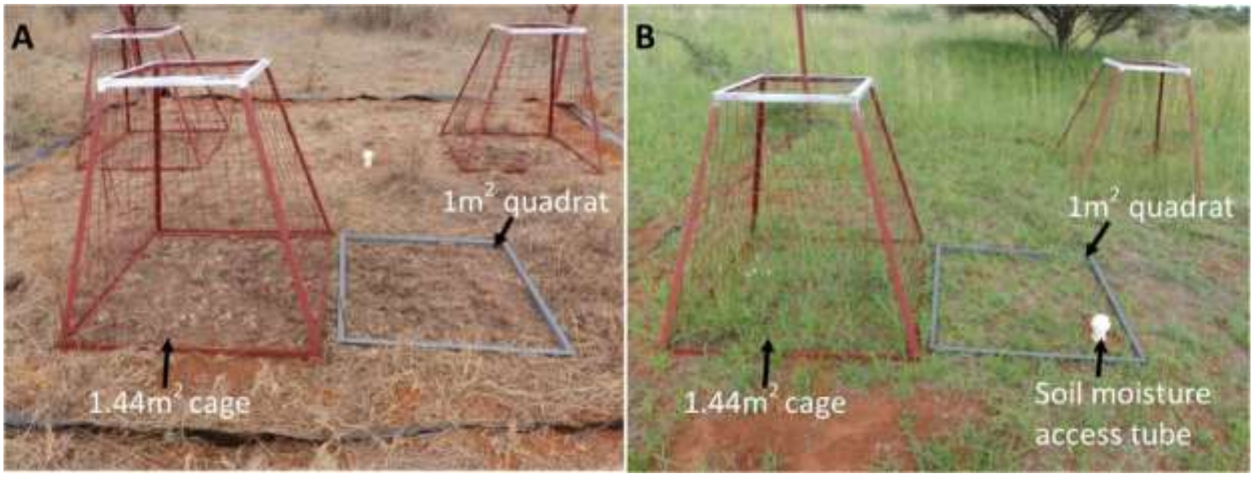


**Figure 3.5** The arrangement of short-term ex-closure (STE) cages and grazed (GRA) quadrats in a grazed treatment under drought conditions (D+G+) is shown in the image. The above images were taken near the end of the 2014 growing season in October (Picture A) and during the 2015 growing season (Picture B) – from Mudongu et al., in prep.

### 3.1.5 Data collection

#### *3.1.5.1 General sampling*

In the first treatment year, through cutting of herbaceous plants in a 1m$^2$ quadrat, biomass was measured at different stages of the growth season, including starting biomass, mid-season biomass, and regrowth biomass. The final output under grazed conditions was referred to as standing biomass, whereas it was referred to as aboveground net primary production in ungrazed conditions (ANPP). Above ground net primary production was measured using both destructive and non-destructive biomass sampling (Ruppert and Linstädter, 2014) to investigate treatment effects on vegetation dynamics: destructive biomass sampling (on STEs), non-destructive sampling via allometric calculations (GRA and LTEs) and (re-) calculation of measured metrics to indices (grazing-offtake, specific ANPP). Aboveground biomass sampling differed between grazed (GRA), short-term ex-closures (STE, = cages), and long-term exclosure plots (LTE, = fences). While GRA and LTEs were always sampled non-destructively, STEs were sampled destructively once a year during peak season. However, at the start of the season, the STEs were cut without sample to eliminate any potential carry-over from past seasons.

To promote synergies between destructive and non-destructive techniques, destructive species-specific biomass sampling per quadrat was paired with measurements of averaged species-specific height and cover, followed by drying and weighing of the cut biomass. Plant material was oven-dried (60C, 48 h), and weighed to the nearest gram. These data were used to establish species-specific allometric equations, which were subsequently used to estimate biomass on the GRA and LTE plots. Each season, Short-Term Ex-closure cages were rotated within the plot to maintain cage production equivalent to that which would have occurred if the cages had not been there.

Biomass was harvested at the end of the growing season (April to May) from 2015 to 2020. During this time, most plant species present on the plots had fully grown and flowered. ANPP was collected destructively from movable cages on grazed plots, whereas standing biomass was measured non-destructively using allometric equations on rested plots (biovolume) (Scurlock et al., 2002, Lauenroth et al., 2006, Ruppert and Linstädter, 2014, Behn et al., In prep.). Biomass cutting and sampling were performed quadrat- and species-wise during the peak-biomass season.

Vital rates of herbaceous species, such as height, growth stage and chlorophyll content, were monitored to examine the impact of drought and grazing on ecosystem function. The determined impact of treatments on the herbaceous layer was used to establish which species were winners and losers, as well as to measure taxonomic and functional diversity. Standing biomass was collected in three $1m^2$ quadrats shielded from grazing by STE movable cages on grazed plots and on ungrazed plots, a total of three sampling quadrats (50 x 50 cm) per plot were used to minimize the impact of destructive sampling on monitoring plots (Linstädter et al., 2013). Species identity, average plant height (5 individuals), predominant phenology and computed percentage total canopy cover for each species were determined prior to harvesting. Furthermore, the canopy cover was classified into living (green plus senescent) and standing dead material (previous year's grey and oxidized plant material). Additionally, the cover of litter, bare ground, and other materials such as manure and stones were estimated at the quadrat-level. Plant material was oven-dried (60C, 48 h), and weighed to the nearest gram.

Soil moisture, soil physiochemical characteristics, and rainfall (measured using an onsite weather station) were all recorded. To evaluate the difference between drought and non-drought treatments, each plot received a single soil moisture access tube. In the experiment, 36 soil moisture tubes were utilized to measure in situ volumetric soil moisture. From December 2013 to the end of the treatment season, measurements were taken weekly at 10 cm depth intervals (maximum depth 70 cm; Diviner 2000, Sentek Technologies). In addition, three 5cm diameter topsoil (0 - 5 cm) core samples were obtained at random locations across the subplots. The study by Mudongo et al. (in prep.) verifies that there are significant soil moisture differences between drought and non-drought treatments.

#### *3.1.5.2 Rationale*

**Pre-growth season cutting:** Cutting of the new STE before the commencement of the growing season was done to create starting conditions that were comparable throughout all STE plots (removing of residual biomass, moribund material etc.). This step was essential if later ANPP estimations are to be justified.

**Pre-growth season cutting of last years' STE plots:** Grazing-offtake was estimated at the conclusion of the following growing season by cutting last year's STE plots in the pre-growth season: The difference between $STE_{new}$ and $STE_{old}$ was recorded as the current season's grazing-offtake.

**GRA plots:** The monitoring quadrats were the GRA plots. As a result, with the exception of the cutting before the first year, they were never destructively sampled.

**Non-destructive estimation of biomass:** To avoid interfering with the given treatments (grazing versus exclusion from grazing) at the relevant plots and quadrats, biomass had to be quantified non-destructively. Destructive biomass measurement would interfere with the plots, confounding (a) the treatments on LTE plots or (b) processes considered to be essential, such as self-shading via senescent and moribund material (LTEs). In addition, it has been repeatedly proved that allometry is a reliable method for estimating the biomass of herbaceous vegetation.

All taxonomic names in this thesis are referenced from World Flora Online (WFO, 2022).

# CHAPTER 4: WHAT CHARACTERIZES WINNER & LOSER SPECIES? EFFECTS OF LONG-TERM DROUGHT & GRAZING

## 4.1 ABSTRACT

Severe drought may trigger a transition of vegetation composition in dryland grasslands, with productive perennial grasses often being replaced by annual grasses. Grazing pressure is thought to exacerbate drought effects, but little is known about the joint effects of grazing and drought on the functional and taxonomic composition of the herbaceous vegetation in African savannas. This study thus aimed to elucidate which herbaceous species and plant functional types (PFTs) are most resistant to prolonged drought and grazing, and whether resting plays a role in this context. Thus, a six-year field experiment was performed in South Africa's Limpopo province, combining drought and grazing treatments. Aboveground herbaceous live biomass was sampled destructively and non-destructively (as described in the previous chapter), and separated into species. Species were grouped into five PFTs, i.e. very broad-leaved perennial grasses, broad-leaved perennial grasses, narrow-leaved perennial grasses, annual grasses, and forbs. For all species, three leaf traits were recorded (leaf area - LA, specific leaf area – SLA, and leaf dry matter content – LDMC) to describe their resource acquisition strategies. Generalized linear models were used to test for treatment effects and their interaction. Association indices were used to detect the relationship between species and treatments. A phenomenon occurs where certain species decline as a result of climate and land-use change (losers) and are replaced by expanding species that thrive in climate-altered environments (winners). Despite the fact that the six-year severe drought had a significant detrimental influence on the biomass production of most species and plant functional types (PFTs), winning species and PFTs were discovered. Moreover, relative winners with increases in relative abundances were detected, mainly forbs and less palatable narrow-leafed grasses with comparatively low LA and high LDMC such as *Aristida stipidata* Hack. These species and PFTs also tended to be favored by grazing. Although few species profited from resting, for most species, the combination of drought and resting proved to be particularly unfavorable. Winners and losers can indicate ecological transition and may be used to guide management decisions.

**Key words:** ANPP, Drought, Grazing, Land-use change, and Plant functional types

## 4.2 INTRODUCTION

Present and ongoing climate change have led to population decline in many species, particularly those with restricted ranges (Staude et al., 2020). Moreover, space-for-time comparisons find significant losses in local diversity worldwide as a result of human disturbance (Newbold et al., 2015). Pacifici et al. (2015) reported that minimization of biodiversity losses on a global scale requires ecologists to identify those species that are likely to be most susceptible to the impacts of climate change. There are hundreds of published, continuing, and new drought experiments occurring globally (Behn et al., In prep., Estiarte et al., 2016, Yahdjian and Sala, 2002). However, drought is extremely understudied in Africa (Hoover et al., 2018). Although grazing management research is well-documented in Africa, there is limited knowledge on the joint effects of drought and grazing on the functional and taxonomic composition of the herbaceous vegetation in African savannas.

Climate change, prolonged drought, and intensive land-use follow two basic paths in impacting biodiversity losses; either through changed biotic interactions (Vandvik et al., 2020) or direct negative effects on species performance and fitness (Krab et al., 2018). On the one hand, intensification of land-use strongly impacts plant communities by causing shifts in taxonomic and functional composition (Busch et al., 2019). On the other hand, community rearrangement may be driven by changes in plant competition, species mortality and recruitment due to water shortages during drought (Bloor and Bardgett, 2012). Generally, land-use may change in a variety of directions with potentially dynamic implications. Although climate and land-use changes are among the top drivers of biodiversity declines (Sala et al. 2000), the core mechanisms underlying such declines at the level of individual populations remain poorly understood (Gea-Izquierdo et al., 2021). Relating species traits to species performance is an effective method that provides a better understanding of the environmental drivers that are most likely responsible for changes in taxonomic composition (Naaf and Wulf, 2011).

Climate extremes, such as severe drought and periods of excessive rainfall, have increased in frequency and magnitude, which has been identified as a crucial expression of climate change (Meehl et al., 2007). As a result, forecasting the effects of climatic extremes on plant functions, communities and ecosystems have become an urgent need in ecology. However, when compared to gradual climate changes, the effects of extreme weather events have received significantly less attention, and knowledge of how extreme climate affects ecosystem services is scarce (Jentsch et al., 2007, Smith, 2011). Currently, the understanding of ecological responses to climate change is primarily based on the impacts of climatic trends such as gradual warming, precipitation change, and $CO_2$ enrichment (Jentsch et al., 2011). Consequently, an approach which enables critical examination of the joint effects of climate extremes and land-use changes, such as drought and intensification of agriculture is accordingly required.

The concept of winner and loser species in the face of climate change is not new (Baskin, 1998, McKinney and Lockwood, 1999), nonetheless, it recently gained the interest of many researchers (Busch et al., 2019, Staude et al., 2020). Winners and losers may be used as indicator species. Indicator species are those that either (i) give evidence for the impacts of environmental change, (ii) provide evidence for the implications of environmental change on other species, or (iii) forecast the diversity of other species, taxa, or communities within an area (De Cáceres, 2013). However, little information has been reported on climate change winner and loser species in African dryland grasslands. This results in a knowledge gap, which has a detrimental effect on the understanding of vegetation dynamics and, eventually, on the development of appropriate rangeland management methods. Therefore, the primary goal of this study was to identify winner and loser species of long-term drought and to, further, assess the effect of resting on species' drought resistance, as well as to test the hypothesis that winner and loser species differ in their trait attributes. If this hypothesis is correct, the discriminating traits would allow for a better understanding of ecological transitions and possibly inform improved management decisions.

**Questions:**

Q1a) Which species and plant functional types are most resistant to prolonged drought and grazing?

Q1b) Does resting have a positive effect on the resistance of the plant functional types and species?

**Hypotheses**

H1a: Drought and grazing will favor stress-tolerant species over ruderal and competitive types, and the abundance of the broad-leaved functional group will decrease while that of the narrow-leaved functional group will increase.

H1b: Most species, particularly competitive ones, will benefit from resting at first; however, the longer a plant species is rested, the more detrimental the resting will be, particularly under drought conditions.

## 4.3 MATERIALS & METHODS

A six-year field experiment was conducted in South Africa's Limpopo province, combining drought and grazing treatments. All herbaceous species were grouped into five plant functional types (hereafter 'PFT'); annual grasses, forbs, narrow-leaved perennial grasses, broad-leaved perennial grasses and very-broad-leaved perennial grasses, following the method described by Linstädter et al. (2014). Furthermore, leaf area (hereafter 'LA'), specific leaf area (SLA) and leaf dry matter content (hereafter 'LDMC') were used, and three of the six plant traits were discovered to be sufficient for capturing functional differences in plant growth, survival and reproduction (Díaz et al., 2016), to find indications of the most likely drivers responsible for winner and loser species, and consequently, herb layer changes in a dry grassland of Limpopo Province, South Africa. ImageJ, was used to calculate leaf area measurement, the software uses a threshold-based pixel count measurement to calculate leaf area (Easlon and Bloom, 2014)

### 4.3.1 Description of Plant Functional Types (PFTs)

Following the method described by Linstädter et al. (2014), herbaceous species were classed into five functional groups based on a hierarchical combination of traits;

(i) Forbs
(ii) Annual grasses
(iii) Narrow-leaved grasses
(iv) Broad-leaved perennial grasses
(v) Very-broad-leaved perennial grasses

These traits relate to life history, growth form and leaf width. This research revealed that three-trait PFTs (e.g. broad-leaved perennial grasses) and two-trait PFTs (e.g. perennial grasses) performed best as indicators of grazing effects in the semi-arid grassland and the arid savanna biome, respectively. Therefore, for this chapter three-trait PFTs method was utilized. The leaf width classification grouped plant leaves based on their size (perennial grasses only), which distinguished narrow-leaved (<5 mm), broad-leaved (5-10 mm), and very-broad-leaved (> 10 mm). Forbs were defined as a plant life form that can include any non-graminoid herbaceous vascular plant (Siebert and Dreber, 2019).

To determine relative winners and losers, all PFTs were grouped per treatment over specific periods. ANPP was calculated as the total biomass production of all PFTs in a specific treatment over one growing season. To determine the relative performance of a particular PFT, the biomass production of that PFT was divided by the total biomass – this, would then, be considered the relative share. Those PFTs whose relative biomass production increased were considered to be relative winners and those which decreased were considered to be relative losers.

### 4.3.2 Traits of winners and losers

To compare the traits of winners and losers of long-term centennial-scale drought, species were selected, based on the sample size of the species in the final year of treatment, representative of each plant functional group. The annual grasses functional group was not statistically comparable due to the lesser sample size and was thus eliminated from this analysis. Firstly, the characteristics of the species that fared the best under drought conditions were compared with those of the species that fared the worst under drought conditions. The species that performed the best under drought conditions were those that produced the most absolute biomass. Secondly, the characteristics of intermediate winners were compared with those of intermediate losers. Intermediate winners were species that had the second best performance on a relative biomass production, and intermediate losers were species that had the second worst performance. For this analysis, traits based on the plant responses to the environment were selected. Because plant leaf economics can disclose a great deal about a plant's adaptation strategy, the following characteristics were selected to compare: Leaf area (LA) and specific leaf area (SLA). For further information on ecological interpretation and the measuring of traits, see Díaz and Cabido (1997) and (Grime et al., 1997).

### 4.3.3 Data collection: biomass and ANPP

Aboveground net primary production was utilized throughout this study to evaluate and portray yearly dryland production in addition to several other important properties of ecosystems.

#### *4.3.3.1 Pre-growth-season treatment*

Prior to the installation of short-term ex-closure cages, all biomass was cut down to 5 cm height on the new STE quadrat as well as on the previous years' STE quadrats in order to establish equal starting points for all cages. Furthermore, STEs were moved from year to year around the plot. To preserve the grass growth, all damage to the grass buds and reproductive tissue was avoided during cutting. All cut biomass was removed from the plots before anchoring of cages. However, it is important to note that no cutting occurred on permanent grazed quadrats (GRA) or long-term ex-closure plots (LTEs). A NADIR-photo of the cut and cleaned quadrat was taken. Date, worker, plot/quadrat, photo-label and total basal area estimates were then noted. The cage was then put in place and anchored thoroughly into the ground with metal anchors to avoid grazing by cattle.

#### *4.3.3.2 Destructive measurements of biomass (on STEs)*

Destructive biomass sampling was carried out at the end of the growth season (every year in mid to end of March/April) on STE quadrats only. Biomass cutting and sampling were performed quadrat- and species-wise during the peak-biomass season. The date, performing worker and plot/quadrat were noted on field sheets. The following data were measured and noted per species (e.g. *Digitaria eriantha*) for all species on the quadrat:

- Species identity
- Average height of plant-individuals (5 measurements)
- Total canopy cover on the quadrat, determined ocurlaly (moribund material was ignored)
- Predominant phenology
- Farthest phenology
- Proportion of green/senescent/moribund biomass (ocular estimate)

All individuals of a single species were cut down to 5 cm and collected in clearly labelled species-specific paper bags. All green and senescent plant material were collected and moribund material was removed from the samples and plots and was not further regarded. Biomass bags were oven-dried (min. 48h at 68°C) and weighed.

#### *4.3.3.3 Non-destructive Estimation of Biomass – Biovolume (on GRAs and LTEs )*

Non-Destructive biomass (Biovolume) sampling was carried out on LTE and GRA quadrats. Measurements were performed quadrat- and species-wise during the peak-biomass season. The data that was recorded is similar to that of the destructive estimation of biomass. No cutting occurs in this sampling.

The methodology for this chapter is described in detail in Chapter 3: Research Methodology.

## 4.4 DATA ANALYSIS

### 4.4.1 Repeated measures ANOVA and Generalized Linear Model (GLM)

The data were examined in two phases using repeated measures ANOVA and GLM. Firstly, the effect of treatment on species and plant functional types were evaluated using drought and grazing as predictor factors. Following that, Tukey's HSD test was used to determine the effect's significance. Second, to examine the influence of time (Year), Drought, grazing and treatment, a repeated measures ANOVA was employed to identify significant associations. The residuals were examined for homogeneity of variance using established techniques (Zuur et al., 2010). Where appropriate, data were in-transformed to ensure that ANOVA assumptions were satisfied. All statistical analyses were conducted in R 4.0.3 using the lsmeans and ggplot2 package (RCoreTeam, 2021).

Biomass production matrices of the four treatments over six sample periods were subtracted (2015 to 2020), to identify species and plant functional types that consistently increased, declined, or stayed constant in biomass production. The rate of change was calculated as the biomass production in the treatments was changing with respect to the control group. Within each growing season, GLM tests were performed to determine if changes in biomass output of each species and plant functional type were significantly different across treatments. The detection of a significant result indicates that the predictor factor had a significant impact on the biomass output of the corresponding species or PFT. Only species with at least five occurrences in both treatments were taken into account. The test ignored plots in which a species was missing in both treatments. A 'loser' was defined as a species or PFT with a significant ($P< 0.05$) average loss in biomass output, whereas a 'winner' was defined as a species or PFT with a significant average increase.

### 4.4.2 Association indices (Indicator species): characterization of winner and loser species and PFTs

To define winner and loser species and PFTs, the association between individual species or PFTs and the various treatments representing habitat types, the ecological preference of the species, and the strength of the association between a given species and treatment were examined. To evaluate these correlations, the phi coefficient of association and the indicator value index (IndVal) were utilized. Furthermore, the Indicator Value index was used to determine which species could be used as indicators of a certain treatment, a method by Dufrêne and Legendre (1997). Calculating the IndVal index between the species and each site group was the first. After this, the approach looked for the group that corresponded to the highest association value. Finally, a permutation test was carried out to investigate whether or not this association was statistically significant.

The indicator value index is the sum of two components known as 'A' and 'B.' (1) Component 'A' is a sample estimate of the chance that the surveyed site belongs to the target site group based on the presence of the species. This conditional probability is known as the specificity or positive predictive value of the species as a site group indicator. (2) Component 'B' is a sample estimate of the likelihood of finding the species in sites in the site group. This second conditional probability is known as the species' fidelity or sensitivity as an indicator of the target site group.

To run an indicator species analysis, species were classed into site groups (treatments) in which they occurred. Using the function multipatt (De Cáceres, 2013) an indicator species analysis was run ($p<0.05$). This function allowed determining lists of species that were associated with particular groups of sites or their combinations. To display the result of the indicator species analysis for all species, regardless of whether the statistical test was significant or not, the significance level was changed in the summary ($p<1$). Pearson's phi coefficient of association, also known as fidelity, was used to determine the association between species and treatments (Chytrý et al., 2002). To calculate an association index such as the component 'A' of IndVal, strassoc was utilized (De Cáceres, 2013). This function allows the possibility to obtain confidence interval limits by bootstrapping and then returns a list with three elements: 'stat', 'lowerCI' and 'upperCI'.

Two steps were taken to characterize winning and loser species using traits associated with environmental changes. First, a univariate test was used to determine if the winner and loser species had distinct trait attributes. For categorical variables, the w2 statistic was used; for numeric variables, the T statistic was used. Secondly, multivariate tests were employed to determine the relationship between different traits. Finally, in the final year of the study (2020), species and PFTs which were positively associated with drought treatments (D+) were considered to be winners of long-term drought, and those negatively associated with this treatment were considered to be losers.

## 4.5 RESULTS

### 4.5.1 Winner and loser plant functional types (PFTs) – absolute biomass

The effect of drought on four plant functional types (PFTs) was compared under grazing conditions; i) Forbs, ii) Narrow-leaved grasses, iii) Broad-leaved grasses, and iv) Very-broad-leaved grasses (Table 4.1). In general, the findings revealed that the number of plant functional types that responded adversely to drought was greater than the number that responded favourably. Forbs exhibited the best drought response, with biomass output 294% more than the non-drought treatment in 2018 (Figure 4.1a). Although the effects of drought on the functional group of narrow-leaved grasses were observed beginning in the third year, this PFT was drought-tolerant over the first two years, making it the second-most drought-tolerant functional group (Figure 4.1c). Surprisingly, from the third observational year through the end of the research period, the impact of drought on narrow-leaved grasses fluctuated. On the other hand, drought had a detrimental impact on the other grass functional groups (Figure 4.1b & d). PFTs' responses to grazing differed across drought and non-drought treatments. Interestingly, while the majority of functional groups succumbed to drought, the rate at which they did so varied. Broad-leaved and very-broad-leaved grasses, on the other hand, appear to be following a distinct pattern: the longer the drought lasted, the greater the drought's impact on these two PFTs. Although these two PFTs responded to drought in similar ways, drought appeared to have had a greater impact on very-broad-leaved grasses, with the control group producing 96% more biomass than the experimental group in the fourth treatment year.

In addition, the effect of drought on the four PFTs mentioned above was also investigated under ungrazed conditions (resting). Long-term grazing exclusion was discovered to slightly improve the response of forbs to drought (Figure 4.2a). In the first year of treatment, the broad-leaved grasses showed a minor improvement in their drought tolerance, as they performed better under drought conditions than under ambient conditions (Figure 4.2b). Overall, the drought response of PFTs was discovered not to differ greatly between grazed and ungrazed plots. Drought, under rested conditions, had a negative influence on all grass functional groups, particularly very broad-leaved grasses (Figure 4.2d), while forbs displayed a greater tolerance to drought. There were, however, some discrepancies that were discovered. Although under resting conditions, forbs performed better under ambient conditions for the first two years, more biomass production under drought conditions was observed from the third treatment year until the sixth year. Overall, under drought conditions, forbs had a slightly higher biomass production under rested conditions. During the first year following treatment, broad-leaved grasses appeared to be drought tolerant. However, the impact of drought on this PFT varied from the second treatment year throughout the research period. The biomass production of the narrow-leaved grasses functional group under rested conditions varied substantially across years (Figure 4.2c), but the production of the very-broad-leaved grasses group decreased continuously as the drought and resting lasted. Overall, forbs and narrow-leaved grasses were the winners of long-term drought, while very-broad-leaved grasses and broad-leaved grasses were the loser PFTs. Moreover, resting proved not to improve species and PFTs' drought resistance. In fact, long-term resting had a strong negative impact on the majority of species and PFTs.

**Table 4.1** This table shows the biomass production (kg) of different plant functional types (PFTs) across different treatments throughout the study period (2015 to 2020).

| PFT | SampYear | D-G- (kg) | D-G+ (kg) | D+G- (kg) | D+G+ (kg) |
|---|---|---|---|---|---|
| Forb | 2015 | 120.60 | 137.80 | 95.67 | 157.73 |
| Forb | 2016 | 81.67 | 175.30 | 24.28 | 131.54 |
| Forb | 2017 | 109.80 | 80.67 | 150.12 | 85.94 |
| Forb | 2018 | 7.20 | 22.70 | 10.53 | 89.40 |
| Forb | 2019 | 58.07 | 63.70 | 202.49 | 104.38 |
| Forb | 2020 | 37.96 | 332.87 | 44.71 | 92.52 |
| HG lan | 2015 | 829.75 | 787.29 | 944.57 | 755.43 |
| HG lan | 2016 | 671.25 | 1701.76 | 289.75 | 1204.58 |
| HG lan | 2017 | 1085.77 | 1271.45 | 660.53 | 476.81 |
| HG lan | 2018 | 205.50 | 710.50 | 31.27 | 156.01 |
| HG lan | 2019 | 931.44 | 777.45 | 311.51 | 60.48 |
| HG lan | 2020 | 546.03 | 850.85 | 63.29 | 89.03 |
| HG lin | 2015 | 202.56 | 94.64 | 121.14 | 156.93 |
| HG lin | 2016 | 105.98 | 183.87 | 101.59 | 298.05 |
| HG lin | 2017 | 497.10 | 227.37 | 283.44 | 39.16 |
| HG lin | 2018 | 48.40 | 134.20 | 47.84 | 39.20 |
| HG lin | 2019 | 173.73 | 246.12 | 55.34 | 42.84 |
| HG lin | 2020 | 50.28 | 352.91 | 39.24 | 44.63 |

| | | | | | |
|---|---|---|---|---|---|
| HG ova | 2015 | 219.56 | 245.06 | 81.66 | 190.85 |
| HG ova | 2016 | 141.56 | 450.59 | 23.94 | 217.87 |
| HG ova | 2017 | 775.88 | 486.50 | 27.76 | 104.40 |
| HG ova | 2018 | 111.40 | 187.10 | 0.00 | 6.80 |
| HG ova | 2019 | 135.06 | 69.80 | 5.69 | 5.60 |
| HG ova | 2020 | 83.18 | 59.17 | 0.20 | 3.28 |

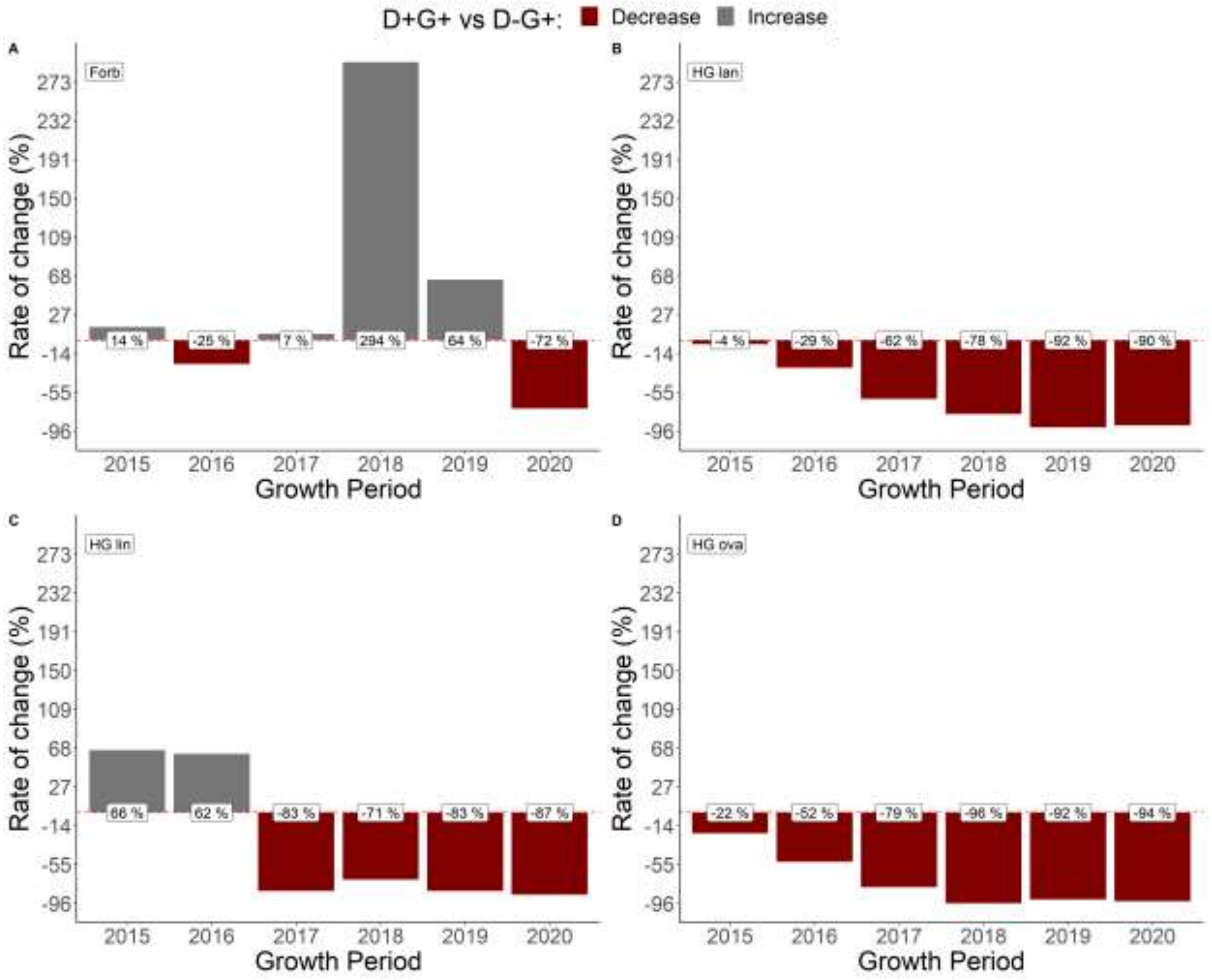


**Figure 4.1.** Change in biomass production percentage between control (non-drought: D-G+) and experimental (drought: D+G+) groups, under grazed conditions over a six-year period. PFTs were described as a shorthand, where; Forb = Forb, HGlan = Broad-leaved, HGlin = Narrow-leaved, HGova = Very-broad-leaved. This figure illustrates the difference in biomass output between experimental and control groups in grazed plots. As stated by the figure titles and growth period, each bar represents the performance of a particular PFT over a specific period. The results that were favorable to the experimental group are presented above the

baseline. Bars below the baseline reflect cases when the control group outperformed the experimental group, with the accompanying negative percentage change.

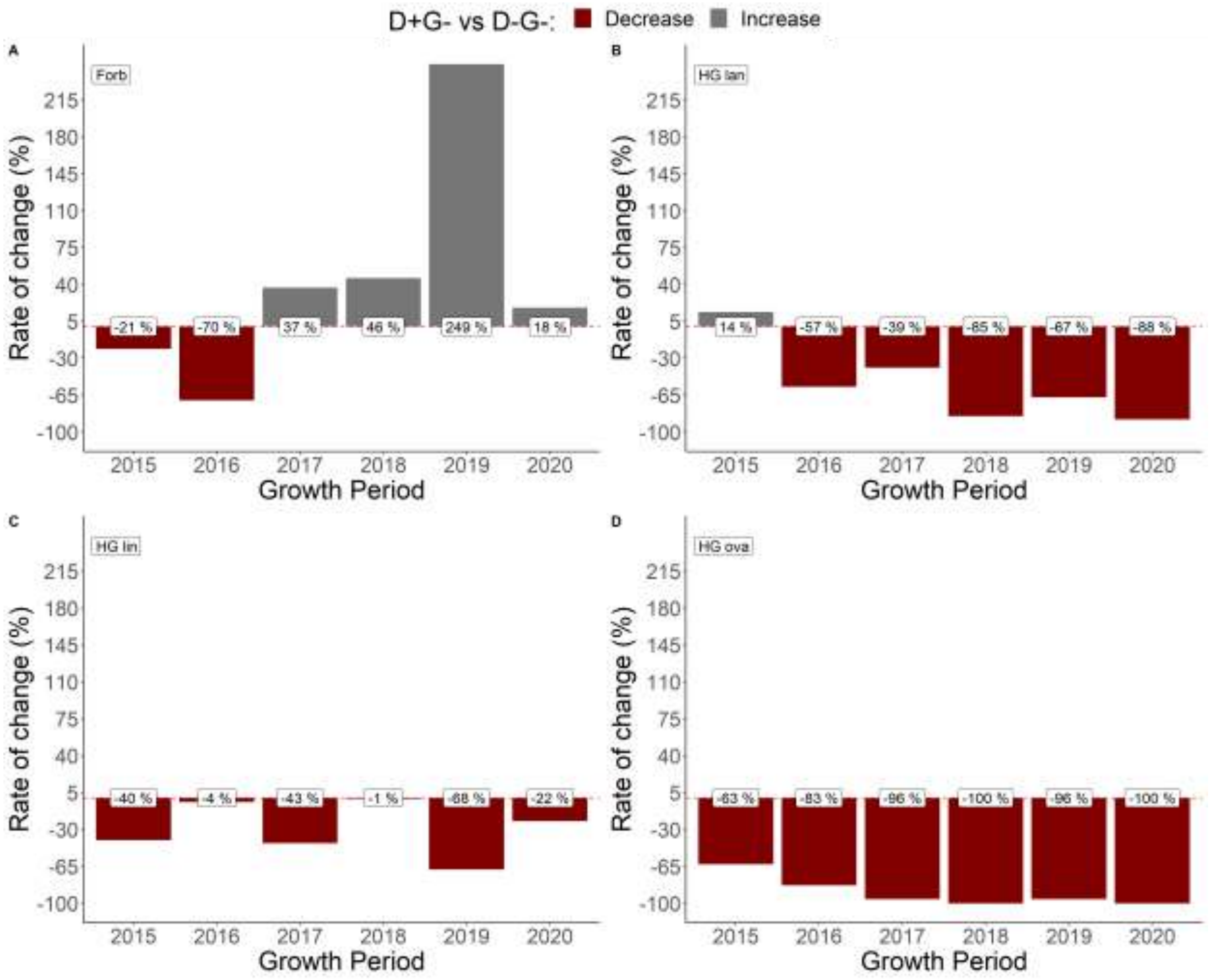


**Figure 4.2.** In this figure, the rate of change of PFTs specific biomass, comparing drought and non-drought treatments under ungrazed conditions are recorded. Each bar shows the percentage change between the control and the treatment group. PFTs where described as a shorthand, where; Forb = Forb, HGlan = Broad-leaved, HGlin = Narrow-leaved, HGova = Very-broad-leaved.

### 4.5.2 Winner and loser plant functional types (PFTs) – relative biomass

Broad-leaved functional groups were found to produce the most biomass under all treatments (Figure 4.3). Nevertheless, under drought conditions, the relative production of biomass tended to decrease with increasing duration of the drought after the second or third growing season, and this trend was observed in both grazed and ungrazed treatments. However, some differences between grazing and rested plots were identified; under rested conditions, a steady decline in relative productivity was observed from the second treatment year to the fourth, after which a slight increase was recorded in the fifth year, which was also followed by a decline. This pattern continued until the sixth year, when a slight increase in productivity was observed again. Under grazed conditions, a decrease in biomass of a comparable magnitude was detected. However, during the first three treatment years a steady increase was recorded, followed by a decline. Nonetheless, the rate of decline was not as evident as it was in the plots that were rested. Under ambient conditions, the relative biomass production tended to be either stable or slightly increased over the study period.

Across all of the experimental treatments, the annual grasses functional group produced the least amount of biomass relative to other PFTs. Annual grasses had the greatest reduction in biomass output, with relative biomass production decreasing from the second to the fifth year and then increasing slightly in the sixth year. However, the biomass production appeared to fluctuate between the different years, across all treatments. There was no discernable pattern of relative biomass production. Very-broad-leaved grasses exhibited the second largest biomass drop. In general, the very-broad-leaved grasses functional group followed a pattern that was quite similar to that of the broad-leaved grasses. This pattern entailed a general decrease in biomass under drought conditions and a steady production of biomass under ambient conditions. The main difference in biomass production was shown under ambient conditions, where a steady biomass output was detected for the first four years, followed by a modest decrease from the fifth to the sixth year under grazing conditions, while there was a more consistent biomass production under rested conditions.

Under drought conditions, forbs and narrow-leaved grasses exhibited an overall relative increase in biomass proportion throughout the study period. Nevertheless, under drought conditions, the production of biomass by forbs was greater when they were grazed, whereas the narrow-leaved grass group produced more when they were allowed to rest. In addition, under natural conditions, a consistent drop in the amount of biomass produced by forbs was detected over the course of the first four years of the experiment. This was followed by a gradual rise in the amount of biomass produced by this PFT in the control treatment (D-G+). Contrastingly, resting under ambient conditions resulted in a constant decline of biomass throughout the study period. In grazed treatments, the proportion of narrow-leaved grasses' relative contribution to the total biomass increased, while in rested conditions, this proportion appeared to be more variable.

Resting impacted the PFTs differently depending on whether there is drought or not. Under drought conditions, broad-leaved and very-broad-leaved perennial grasses immediately declined in productivity from the second year throughout the study period. However, under ambient conditions, broad-leaved and very-broad-leaved grasses initially profited from resting but as the drought period lengthened the impact became negative; very-broad-leaved grasses increased in relative productivity from 2015 to 2018, whereas broad-leaved grasses profited for two years (2015 & 2016).

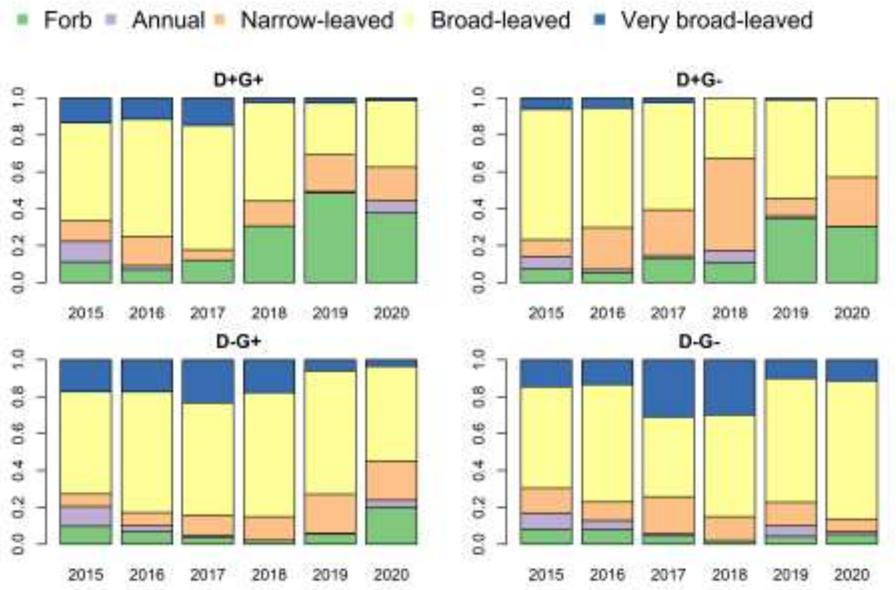


**Figure 4.3.** Plant functional types' relative share of biomass under drought (D+) and non-drought (D-) conditions from grazed (G+) and ungrazed (G-) treatments over time. This figure illustrates the different PFTs' relative share of biomass (proportions) to the aboveground net primary production of a particular treatment over a specific time period. The x-axis represents the year while the y-axis represents the biomass proportion.

**Table 4.2.** Summary of repeated measures ANOVA comparing PFTs biomass production, corresponding to the year, drought, grazing and treatment. Significant codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1 Non-significant ‘ns’

| PFT | Effect | DFn | DFd | F | p | Significance |
|---|---|---:|---:|---:|---:|---|
| Annual | Year | 5 | 15 | 15.327 | 0.000 | *** |
| Forb | Year | 5 | 15 | 0.936 | 0.486 | |
| Broad-leaved | Year | 5 | 15 | 3.824 | 0.020 | * |
| Narrow-leaved | Year | 5 | 15 | 1.287 | 0.320 | |
| Very-broad-leaved | Year | 5 | 15 | 3.004 | 0.045 | * |
| Annual | Treatment | 3 | 15 | 2.410 | 0.108 | |
| Forb | Treatment | 3 | 15 | 0.931 | 0.450 | |
| Broad-leaved | Treatment | 3 | 15 | 5.761 | 0.008 | * |
| Narrow-leaved | Treatment | 3 | 15 | 1.221 | 0.336 | |
| Very-broad-leaved | Treatment | 3 | 15 | 4.093 | 0.026 | * |
| **PFT** | **Drought** | | **statistic** | **df** | **p** | **p<.05** |
| Annual | n | y | 3.374 | 11 | 0.006 | ** |
| Forb | n | y | 0.123 | 11 | 0.904 | ns |
| Broad-leaved | n | y | 5.360 | 11 | 0.000 | *** |
| Narrow-leaved | n | y | 2.414 | 11 | 0.034 | * |
| Very-broad-leaved | n | y | 3.355 | 11 | 0.006 | ** |
| **PFT** | **Grazing** | | **statistic** | **df** | **p** | **p<.05** |
| Annual | n | y | -0.759 | 11 | 0.464 | ns |
| Forb | n | y | -1.525 | 11 | 0.155 | ns |
| Broad-leaved | n | y | -1.532 | 11 | 0.154 | ns |
| Narrow-leaved | n | y | -0.236 | 11 | 0.818 | ns |
| Very-broad-leaved | n | y | -0.829 | 11 | 0.425 | ns |

### 4.5.3 Species-specific performance – relative winners and losers

The effects of drought and grazing on all of the herbaceous species found in the DroughtAct experiment were evaluated. However, only a few species that proved to be good indicators of the environmental conditions were chosen for visualization. In general, drought was adversely related to the majority of species while grazing was favourably associated with them (Figure 4.4a-b). A few species, however, exhibited the opposite reaction to treatment. *Dactyloctenium aegyptium* and *Tragus berteronianus*, both annual grasses, exhibited the highest association with drought among the species studied. *Dicoma tomentosa* showed a neutral response to drought while *Limeum viscosum*, on the other hand, demonstrated a slight positive association. Interestingly, the majority of the species adversely affected by grazing have broad leaves. Surprisingly, *Aristida congesta* and *Chamaecrista mimosoides* displayed similar reactions to both treatments, including an aversion to drought and a significant association with grazing. Both species, interestingly, have narrow leaves.

To assess the combined effect of drought and grazing, the relationship between treatment types and species was examined (Figure 4.5). Under ambient conditions, the majority of species were more favourably related to grazing (D-G+: control treatment) than to resting (D-G-). However, several species were positively related to resting. Under ambient conditions, only two species were positively related to both grazing and resting conditions, *Digitaria eriantha* and *Heteropogon contortus*. Interestingly, all of the species that benefited from resting had wide leaves. Surprisingly, even under drought conditions, the majority of species were better associated with grazing (D+G+) than with resting (D+G-). *Dactyloctenium aegyptium* and *Tragus berteronianus* had the strongest correlation with drought and grazing treatment (D+G+). They were, however, negatively associated with other treatments.

**Table 4.3.** Summary of indicator value components of species using an R function called '*IndVal.g'* from the indispecies package. Data from the final year of treatment (2020) was utilized. The indicator value index is a combination of two components labeled 'A' and 'B.' Component 'A' is a sample estimate of the likelihood that the surveyed site belongs to the target site group given the presence of the species. Component 'B' is a sample estimate of the likelihood of finding the species in the site group's sites.

| **Non-Drought & Resting (D-G-)** | | | | |
|---|---|---|---|---|
| **Species** | **Plant Functional Type** | A | B | p-value |
| *Panicum maximum* | Very-broad-leaved grass | 1.000 | 0.0833 | 1.000 |
| *Phyllanthus parvulus* | Forb | 1.000 | 0.0833 | 1.000 |
| **Non-Drought & Grazing (D-G+)** | | | | |
| **Species** | **Plant Functional Type** | A | B | p-value |
| *Aristida congesta* | Broad-leaved grass | 0.922 | 1.000 | 0.001 *** |
| *Chamaecrista mimosoides* | Forb | 0.810 | 1.000 | 0.001 *** |
| *Aristida diffusa* | Narrow-leaved grass | 0.943 | 0.750 | 0.001 *** |
| *Brachiaria nigropedata* | Broad-leaved grass | 0.821 | 0.750 | 0.003 ** |
| *Pogonarthria squarrosa* | Broad-leaved grass | 0.902 | 0.667 | 0.002 ** |
| *Trichoneura grandiglumis* | Broad-leaved grass | 1.000 | 0.583 | 0.001 *** |
| *Seddera suffruticosa var hirsutissima* | Forb | 0.857 | 0.667 | 0.001 *** |
| *Chamaecrista absus* | Forb | 0.746 | 0.750 | 0.002 ** |
| *Schkuhria pinnata* | Forb | 0.776 | 0.667 | 0.002 ** |
| *Cyperus ruprestris* | Forb | 1.000 | 0.417 | 0.001 *** |
| *Eragrostis superba* | Broad-leaved grass | 0.993 | 0.417 | 0.002 ** |
| *Tricholaena monachne* | Broad-leaved grass | 0.914 | 0.250 | 0.111 |
| *Dactyloctenium aegyptium* | Annual grass | 1.000 | 0.167 | 0.22 |
| *Corchoris asplenifolius* | Forb | 1.000 | 0.167 | 0.205 |
| *Oxygonum alatum* | Forb | 1.000 | 0.167 | 0.201 |
| *Themeda triandra* | Broad-leaved grass | 0.886 | 0.167 | 0.361 |
| *Chloris virgata* | Narrow-leaved grass | 1.000 | 0.083 | 1.000 |
| **Drought & Grazing (D+G+)** | | | | |
| **Species** | **Plant Functional Type** | **A** | **B** | **p-value** |
| *Dactyloctenium aegyptium* | Annual grass | 1.000 | 0.417 | 0.003 ** |
| *Limeum viscosum* | Forb | 0.787 | 0.417 | 0.016 * |
| *Tragus berteronianus* | Annual | 0.960 | 0.333 | 0.009 ** |
| *Urochloa mosambicensis* | Very-road-leaved grass | 1.000 | 0.083 | 1.000 |
| *Eragrostis lehmaniana* | Narrow-leaved grass | 1.000 | 0.083 | 1.000 |
| **Drought & resting (D+G-)** | | | | |
| **Species** | **Plant Functional Type** | **A** | **B** | **p-value** |
| Dicoma tomentosa | Forb | 1.000 | 0.100 | 0.194 |

**Group Combination A: D-G- & D-G+**

| Species | Plant Functional Type | A | B | p-value |
|---|---|---|---|---|
| *Digitaria eriantha* | Very-broad-leaved grass | 0.976 | 0.833 | 0. 001 *** |
| *Heteropogon contortus* | Broad-leaved grass | 0.988 | 0.542 | 0.006 ** |
| *Melinis repens* | Annual grass | 0.958 | 0.250 | 0.194 |
| *Bidens pilosa* | Forb | 1.000 | 0.083 | 1.000 |

### 4.5.4 Traits of winner and loser species

There appears to be a discernable trait pattern between winners and losers. In general, relative winners of long-term drought, such as forbs and narrow-leaved perennial grasses (represented by *Aristida stipitata* and *Chamaecrista mimosoides*, respectively), have lower leaf area and greater mean specific leaf area, although the difference is not statistically significant (Figure 4.6). However, leaf dry matter content (LDMC) appears to be highly variable between the winners and losers of long-term drought.

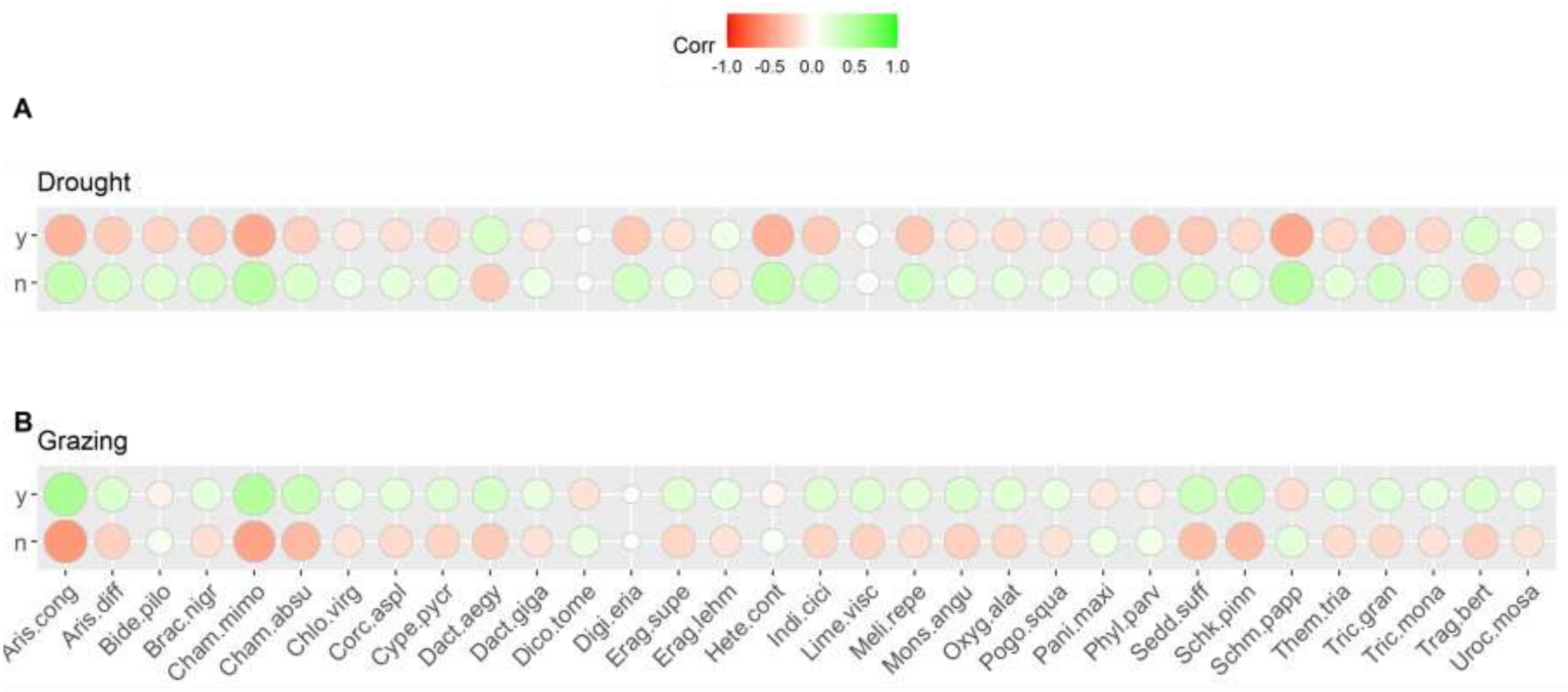


**Figure 4.4.** Strength of association between species and treatment; Drought and Grazing. Note, that the size and the intensity of the colour of the circle represent the strength of association; big circles represent a strong association while smaller circles represent weaker correlation. The red colour represents a low/negative association, white represents neutrality and green represents a high/positive association. Where y = yes and n = no.

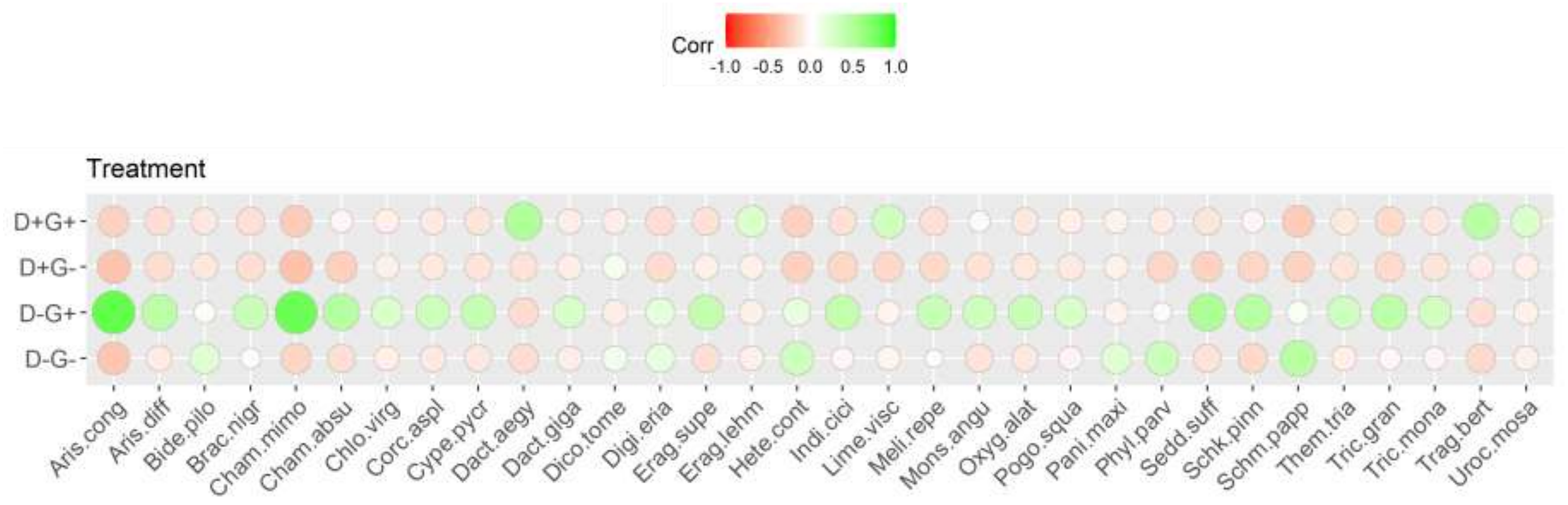


**Figure 4.5.** This figure compares the strength of association between species and different treatments. The three colours represent low, medium and high associations between species and treatment groups.

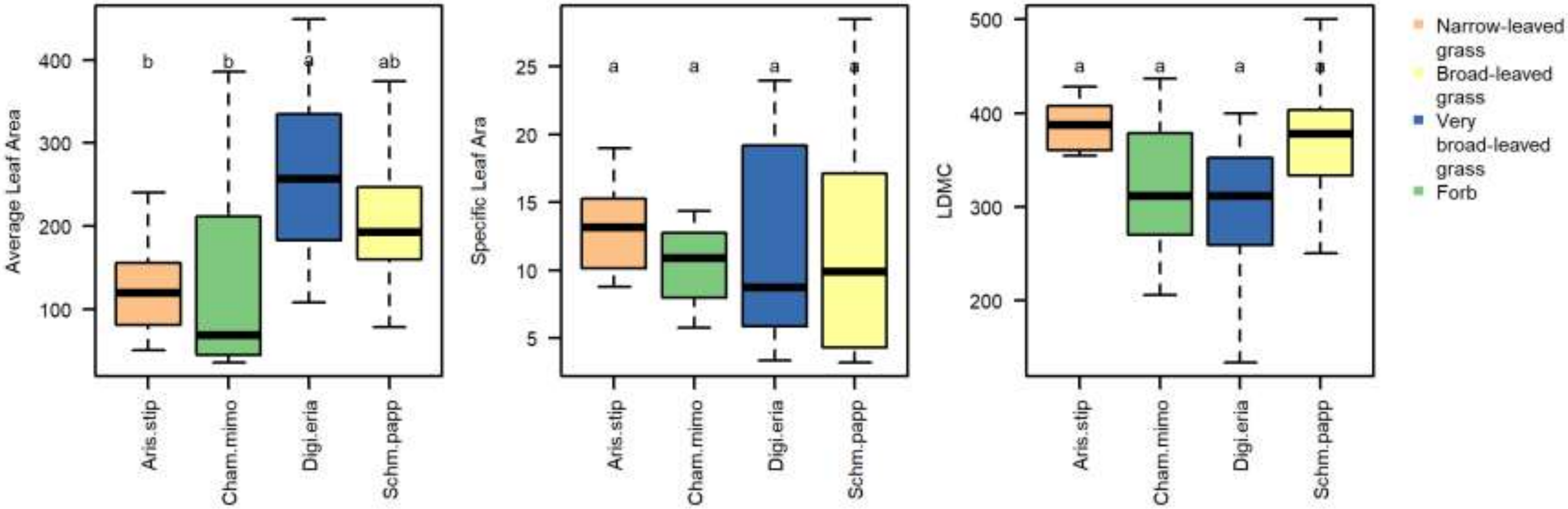


**Figure 4.6.** This figure compares the average leaf area (LA), specific leaf area (SLA), and leaf dry matter content (LDMC) of a selected herbaceous species in the DroughtAct experiment, in the final treatment year (2020).

## 4.6 DISCUSSION

The analyses of results indicated that long-term drought and grazing may have a detrimental effect on the biomass production of the majority of both plant species and plant functional types (‘Losers’), with only a few species and PFTs found to profit (‘Winners’).

The study hypothesized that drought and grazing would favor stress-tolerant species over ruderal and competitive types, and that the abundance of the broad-leaved functional group would decline while the abundance of the narrow-leaved functional group would increase (H1a). This hypothesis can be confirmed. Also, it is in line with CSR theory by Grime (1977), which suggests that the variables that prevent the resolution of competition are stress and disturbance, which in this study were drought and grazing, respectively. Hence, long-term drought favoured stress-tolerant species. This was mainly because both stress and disturbance can suppress plant development to the point where individual plants barely interfere with one another and competition is eliminated (Grime, 1974). However, the decline in productivity was anticipated as manipulated precipitation decreases have been reported to slow plant development, particularly the accumulation of biomass and aboveground net primary productivity (Liu et al., 2015).

These findings, further, revealed that the number of plant functional types that responded adversely to drought was greater than the number that responded favourably. The majority of plant functional types were not drought resistant. This correlates with McKinney and Lockwood (1999)’s findings who also observed a low percentage of winners; the percentage of native species that are winners in localized disturbances ranges from 5% to 29%. However, the numbers of winners decrease as the severity of disturbance increases. This would imply that the degree of the imposed stress may also result in a similar response — that the more severe the stress, as is the case in the DroughtAct experiment, the fewer winners should be anticipated. New evidence suggests that the majority of species are disappearing as a direct result of human activities (referred to as "losers"), and they are being succeeded by a much smaller number of expanding species that can thrive in environments that have been altered by humans (referred to as "winners") (McKinney and Lockwood, 1999).

Forbs displayed the strongest resistance to drought and grazing over an extended period, followed by narrow-leaved grass. Similarly, Heitschmidt et al. (2005) found that the relative impacts of both drought and grazing treatments generally followed a distinct pattern: cool-season perennial grass was the most negatively impacted by drought, followed by annual grass, warm-season perennial grass, and forbs, respectively. It may be hypothesized that a higher abundance of forbs at the scale of measurement is a result of increased level of disturbance from livestock and water stress, which i) creates niches for the establishment of weedy species and ii) increases the patchiness of the environment, creating opportunities for different functional groups of species. Moreover, the DroughtAct experiment was under moderate grazing pressure and also followed a rotational grazing scheme. Hence, a stronger grazing pressure might have had a lesser beneficial effect on many of the species.

The study also confirmed the hypothesis that resting initially benefits competitive species, but the longer it persists, the more detrimental its effects on plant species become, particularly under drought conditions. Although few species profited from resting, for most species, the combination of drought and resting proved to be particularly unfavorable. Mudongo et al. (in prep.) also discovered that an appropriate rest period is one growing season, even under acute drought conditions, because increased rest periods result in decreased biomass output and ultimately, veld degradation. The majority of the herbaceous species were negatively associated with drought and generally preferred to be grazed than rested. Under conditions of rest, drought had a detrimental effect on all grass functional groups, particularly very-broad-leaved grasses, but forbs exhibited a stronger resilience to the effects of the drought. In general, forbs perform well during prolonged droughts (O'Connor, 1998), owing to their wide range of functional features, notably those related to disturbance tolerance, optimal resource acquisition, and limited resource requirement (Wesuls et al., 2013). The biomass production of the narrow-leaved grasses functional group under rested conditions varied substantially across years, but the production of the very-broad-leaved grasses group decreased continuously as the drought and resting lasted.

*Dactyloctenium aegyptium* and *Tragus berteronianus*, both annual grass, were the most resistant grass species, while *Limeum viscosum* and *Indigofera cicinnata* were the most drought-resistant forbs. These findings agree with Pfeiffer et al. (2019) who also discovered that grazing and aridity reduced the abundance of perennial grass, furthermore, rangeland productivity reduced and annual grass abundance increased as a consequence of increased aridity and grazing intensity. Livestock preferred perennial over annual grasses at low grazing intensities; preference switched to annual grasses at intermediate intensities, and became non-discriminating at high grazing intensities (Mudongo et al., in prep.). The specific leaf area (SLA), the amount of aboveground living biomass, and the ratio of living to dead biomass all have an impact on the likelihood that a particular grass patch will be grazed (Pfeiffer et al., 2019).

When comparing the different PFTs, forbs and narrow-leaved grasses functional groups were found to be the most tolerant to drought whereas, broad-leaved and very-broad-leaved grasses classes were highly susceptible to the impacts of drought. The observed differences in response to both drought and grazing can be largely attributed to their functional traits. Based on their leaf economics and resource acquisition strategies, broad-leaved and very-broad-leaved grass fall within the competitive class under the CSR triangle by Grime (1977). Hence the longer the drought lasted, the greater the drought's impact on these two PFTs. Despite the fact that these two PFTs responded to drought in similar ways, drought appeared to have had a greater impact on very-broad-leaved grasses, with the control group producing 96% more biomass than the experimental group in the fourth treatment year.

## 4.7 CONCLUSIONS

The study demonstrated that long-term drought results in fewer winners than losers. Nonetheless, winners and losers of drought were detected, and it was found that the key functional features that distinguish winners and losers are linked to disturbance tolerance, optimal resource acquisition, and low resource requirement such as low leaf area and high leaf dry matter content. Under drought conditions, the observed reduction in biomass production from the losers of drought, broad-leaved and very-broad-leaved functional groups, was a clear indicator that long-term drought caused veld degradation regardless of whether the veld was grazed or not. This was due to the fact that in dryland grasslands, the broad-leaved and very-broad-leaved functional groups produce the most biomass. Moreover, long-term resting proved to have a negative impact on species and PFTs' drought resistance. Furthermore, the fact that drought winners, forbs and narrow-leaved grasses, tended to have different characteristics from drought losers suggests that plant functional traits could be employed as early markers of veld degradation. This would enable prompt management interventions and, eventually, improved utilization of natural resources.

These findings add to the current body of knowledge for explaining the establishment of communities and species composition in the face of changing climatic conditions and land-use patterns. Moreover, this approach can also be employed by researchers working in other managed habitats, as the DroughtAct experiment is uniquely capable of quantifying plant species-specific responses or resistance to the effects of climate change. As a result, this chapter will assist other researchers in determining ecological winners and losers, which will allow for a better understanding of the core mechanisms underlying biodiversity declines and will consequently contribute to the solution of the detrimental impacts that climate change has had on dryland grasslands.

The next chapter evaluates the impact of drought, grazing and resting on taxonomic and functional diversity.

# CHAPTER 5: EFFECT OF DROUGHT, GRAZING AND RESTING ON FUNCTIONAL AND TAXONOMIC DIVERSITY

## 5.1 ABSTRACT

It is projected that extreme climatic conditions such as drought would have a significant detrimental effect on all levels of biodiversity, and that this loss of biodiversity will likely have an effect on the structure and function of ecosystems. It is well known that grazing and other types of disturbances, especially those that are intensive, are among the leading causes of biodiversity loss in Africa's ecological systems. Furthermore, little research has been conducted on the effect of drought and grazing on taxonomic and functional diversity in dryland grasslands. As a result, the purpose of this study was to investigate the effects that drought, grazing, and resting have on the diversity of herbaceous species. To achieve this objective, a field experiment called DroughtAct was conducted in Limpopo province, South Africa, between 2014 and 2020. In this experiment, severe and extended drought treatments were combined with moderate grazing, and the ecosystem functions and services derived from grazed (G+) and rested (G-) vegetation were compared and contrasted under drought (D+) and ambient (D-) conditions. The identification and recording of herbaceous plant species, as well as their abundance and occurrence, were performed annually. In addition, species were categorized into functional groups according to their growth form, which included forbs, annual grasses, very-broad-leaved perennial grasses, broad-leaved perennial grasses, and narrow-leaved perennial grasses. To determine the effects of treatments on species diversity, Analysis of variance (ANOVA) was implemented using R. Overall, the study showed that extended periods of drought and grazing negatively impacted both taxonomic and functional diversity. In addition, the negative effects of drought worsened and were more apparent as the duration of the drought increased. In general, drought treatments reduced taxonomic and functional richness, species per unit area, and resulted in higher species evenness. The increased species evenness can be linked to a decline in the abundance of the dominant species which caused the distribution to become more equal. Additionally, it was discovered that resting had diverse effects on the various diversity indices; for example, resting had a negative effect on species richness almost immediately, although its effect on Shannon diversity was not apparent until the drought period lengthened.

**Keywords:** Functional divergence, functional richness, species richness, species evenness, Shannon wiener index

## 5.2 INTRODUCTION

The world faces a significant problem in the form of climate change, which is already impacting the natural ecosystems and biodiversity of the planet (Sintayehu, 2018). Increased biodiversity is reported to improve ecosystem functioning and services (Loreau, 2010). Therefore, understanding the effect of drought and grazing on functional and taxonomic diversity is critical for conservation strategy development and resource management; unfortunately, expertise in this area is sparse (Díaz et al., 2007). Despite appearances, disturbance, such as grazing, forms an integral part of any ecosystem, Connell (1978) coined a term called 'intermediate disturbance hypothesis' (IDH) which states that species diversity would be the highest at a moderate intensity of disturbance. Biswas and Mallik (2010) discovered that functional diversity matched the IDH predictions, as species richness and diversity, as well as functional richness and diversity, peaked at moderate disturbance intensity.

Functionally deterministic assembly implies that future post-disturbance changes in biodiversity, as well as related ecosystem variables, could be forecasted using species' functional properties (Purschke et al., 2013). Both dominant species traits and trait distribution within species play an essential role in modifying the consequences of global changes on ecosystem processes (Xu et al., 2018). When investigating a given function under a certain set of climatic conditions, species may seem functionally redundant; nevertheless, this is factually inaccurate, as numerous species are needed at various times and locations in the face of climate change to sustain the ecosystem's multi-functionality (Isbell et al., 2011).

Diverse grassland plant communities may retain production better than low-diversity communities in the face of severe climatic events because they are more resistant to drought, change less, and exhibit more resilience, with faster recovery rates following drought (Tilman and Downing, 1994). In support of these findings, Isbell et al. (2015)

showed that the production of low-diversity communities decreased by around 50% during severe climatic events, whereas that of high-diversity communities decreased by approximately 25%. Although the intermediate disturbance hypothesis (IDH) has offered a basic understanding of the relationship between disturbance and species diversity, research on the relationship between disturbance and functional diversity is lacking (Biswas and Mallik, 2010).

Tilman et al. (2001) defined functional diversity as an organism's value and variety of functional traits in a particular environment. To comprehend the processes behind the association between diversity and ecosystem function, it is necessary to narrow down the idea of diversity. Moreover, the relationship between diversity and ecosystem function is worth investigating because changes in plant functional diversity, expressed as relative abundance, value, and range of plant functional traits in an environment, may reveal significant changes in biodiversity (Díaz et al., 2007). Niche complementarity is a positive interaction between species induced by interspecific differences in resource demands, as well as temporal and spatial differences in resource and habitat utilization (Mulder et al., 2001). Tilman et al. (1997) postulated that productivity may be greater in environments with greater species diversity owing to "niche complementarity" among various species combinations and the increased possibility of such combinations occurring in environments with greater species diversity. Furthermore, niche complementarity has been suggested as a potential pathway linking diversity to ecological processes (Tilman et al., 2001).

'Disturbance,' according to Mouillot et al. (2012), is any human- or natural-caused event that causes localized and transient changes in species demographic rates. Anthropogenic disturbance is becoming a primary driver in many ecosystems (Hoekstra et al., 2005), possibly affecting ecosystem function as well as plant biodiversity (Bellard et al., 2012, Sintayehu, 2018, Isbell et al., 2011). Disturbance may be classified into three types. (i) biotic pressure, which is often brought by foreign species; (ii) environmental changes, such as habitat degradation and changes in abiotic conditions; and (iii) anthropogenic factors (Mouillot et al., 2012). The impact of disturbance on an ecosystem is often reflected in reduced reproduction rates and increased mortality rates of resident species, resulting in a density-dependent competition with less influence on community structure (Holt, 1985). The disturbance may severely lower species abundance or exclude species with certain qualities; in such cases, trait variability across species may be the deciding factor in their response to disturbance (Haddad et al., 2008).

At the conception of this chapter, the following research questions were raised:

**Q1:** What is the impact of long-term drought and grazing on functional and taxonomic diversity over time?

**Q2:** How do different diversity indicators change over time?

**Q3:** Can patterns of diversity modifications be observed?

**Hypotheses**

**H1:** Functional and taxonomic diversity will decrease over time, particularly in response to the combined effect of drought and grazing

**H2:** The longer the drought period lasts, the greater the differences will be between treatments or between years

**H3:** The highest taxonomic and functional diversity will occur at intermediate levels of drought and grazing

## 5.3 MATERIALS & METHODS

### 5.3.1 Study region

The experimental set-up, location and data collection are similar to those in **Chapter 4** and are described in detail in chapter 3.

### 5.3.2 Data collection and analysis

The data set had short-term ex-closure cages (1 $m^2$) unique identifier within each treatment that was maintained in the six years of data collection denoted by CageId=1,2,...285. The diversity calculations were based on percentage cover as an abundance measure. The treatment was a categorical variable denoted by Treatment with D-G+, D-G-, D+G-, and D+G+ as groups. The year variable was an ordinal which had equally distanced space and was denoted by Year=1,2,3,4,5,6, where values 1, 2, 3, 4, 5, and 6 mark the years 2015, 2016, 2017, 2018, 2019 and 2020, respectively. The data were examined in two phases. Firstly, the following three diversity indices were calculated; a) Species richness, b) Shannon-Wiener Index, and c) species evenness, using the "diversity" function of the "vegan"- package (Oksanen et al., 2020).

To quantify the impact of long-term drought, grazing and resting on biodiversity, diversity proxies such as species richness, species evenness, functional richness, evenness and divergence, Shannon-Wiener index etc., need to be clearly defined and calculated.

**Species Richness** - a site's species richness can be defined as the number of taxonomic levels, including species, that are present per unit area (Brown et al., 2007). Species-rich sites are those that have a greater number of taxonomic species. These sites are likely to be more biologically complex, and they may even be more significant from both an environmental and an ecosystem functionality perspective. In this analysis, species richness was calculated as the number of species recorded per sampling quadrat (1 m$^2$).

**Shannon-Wiener Index (H')** - is an information index and is the most commonly used diversity index in ecology. Technically, the Shannon-Wiener Index quantifies the uncertainty associated with predicting the identity of a new taxa given the number of taxa and evenness in the abundance of individuals within each taxon.

**Equation 1**

$$H' = -\sum \left( \frac{ni}{N} \; X \ln \frac{ni}{N} \right)$$

Where *ni* is the number of individuals or amount (biomass) of each of the *I* species and *N* is the total number of individuals (or biomass) for the site.

The value of H is directly proportional to diversity. The lower the value of H, the lower the diversity. The higher the value of H, the higher the diversity of species in a community. Values of *H′* can range from 0 to 5, although they typically range from 1.5 to 3.5.

The Shannon-Wiener Index assumes that the sample for site was collected randomly.

**Species Evenness** – evenness is a measure of how homogeneous or even a community or ecosystem is in terms of the abundance of its species. A community in which all species are equally common is considered even and has a high degree of evenness.

**Species accumulation curve** – an important aspect of species richness is the sampling effort required to discover the maximum number of species per site. It is clear that the longer the sampling period the higher the likelihood of discovering more species. A species richness (accumulation) curve greatly encapsulates this concept. The species accumulation curve plots the total number of detected species against the total number of quadrats, which is considered to be a measure of the sampling effort. The point at which the species richness curve levels off (asymptote) may be used to estimate the richness, this was performed using the “diversity” function of the “specaccum”- package, using the ‘random’ method (Oksanen et al., 2020).

**Pilou evenness (*J*)** compares the actual diversity value (such as the Shannon-Wiener Index, *H'*) to the maximum possible diversity value (when all species are equally common, *Hmax=ln s* where *S* is the total number of species). For the Shannon-Wiener Index, the Pielou evenness (*J*):

**Equation 2**

$$J = \frac{H'}{H_{max}}$$

$$= \frac{H'}{\ln S}$$

Pielou evenness (*J*) is constrained between 0 and 1.0 and the more variation in abundances between different taxa within the community, the lower *J*. Unfortunately, Pilou's *J* is highly dependent on sample size (since *S* - the estimated number of species is dependent on sampling effort) and is also highly sensitive to rare taxa.

**Diversity shift** – the diversity metrics defined above represent the measures of the diversity (true diversity) of taxa within a given treatment. This is also known as alpha diversity. To measure the diversity change between different treatments, beta diversity was employed across different years. Beta diversity measures the change in diversity between habitats or ecosystems and is thus a measure of spatial turnover of species and it is expressed as the number of unique species (species only present in one of the treatments) between the ecosystems and thus measures the change in species diversity between treatments. In order to compare treatments, diversity was measured between each pair of sites, yielding a matrix of beta-diversity indices. This matrix was a triangular (distance) matrix as the diagonals (a site compared to itself) will be 0 and the upper right half of the matrix will be a mirror of the lower left half. To visualize these differences in diversity between treatments a principal coordinate analysis was used, from the R function “pco”, package ‘labdsv’ (Roberts, 2007). For the distance matrix, the function ‘vegdist’ from ‘vegan’ package was used with the quantitative bray Curtis index (Oksanen et al., 2020).

The functional distances between the species (needed to calculate the Functional diversity index) were based on the 3 leaf traits (LA, SLA and LDMC); reproductive and vegetative height. All traits for each species were averages from samples taken at the study site. The distance matrix then was based on Euclidean distance. Mason et al. (2005) narrowed functional diversity into three basic components: functional richness, functional evenness, and functional divergence, and defined them as follows ;

**Functional richness** – the proportion of niche space occupied by species in the community. A low functional richness suggests that a significant portion of the resources that may be accessible to the community are not being utilized.

**Equation 3**

$$\mathrm{FR_{ci}} = \frac{\mathrm{SF_{ci}}}{\mathrm{R_C}}$$

where $FR_{ci}$ = the functional richness of functional character c in community i,

$SF_{ci}$ = the niche space filled by the species within the community,

$R_c$ = the absolute range of the character.

**Functional evenness** – the uniformity with which abundance is distributed in a populated niche area. A lower functional evenness indicates that some areas of the niche space, despite being occupied, are not being utilized to their maximum capacity, assuming that the niche space has uniform resource availability.

**Functional divergence** – the degree to which abundance distribution may optimize functional trait differences in community niche areas. When there is a high functional divergence, there is also a high degree of niche differentiation, which results in minimal resource competition.

**Equation 4**

$$\mathrm{FD_{var}} = \frac{2}{\pi}\mathrm{arctan}\left[5\ \mathrm{X} \sum_{\mathrm{i}=1}^{\mathrm{N}} [(\ln \mathrm{Ci} - \ln \mathrm{x})^2\ X]\right]$$

where FDvar = the functional divergence across functional character categories,

Ci = the character value for the ith functional character category,

Ai = the proportional abundance of the ith functional character category,

ln x = the abundance-weighted mean of the natural logarithm of character values for the categories. That is the sum of category proportional abundances multiplied by the natural logarithm of category character values.

The arc tangent is taken from the abundance-weighted sum of squares for the categories, and multiplied by 2/π so that the index is constrained to vary between 0 and 1.

This sub-division of functional diversity follows species diversity definitions by Purvis and Hector (2000), categorized into (i) species richness and (ii) evenness in species abundance. Richness and evenness change independently, although referring to the same entities – species (Mason et al., 2005). ‘dbFD’ function of the FD package was used to calculate all these indices (Villéger et al., 2008), where ‘dbFD’ returns the three

FD indices: functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv).

In the next step analysis of variance (ANOVA) was utilized. To measure the impact of treatment on diversity, the effect of treatment on richness, Shannon and evenness were evaluated. After that, the Tukey's HSD test was utilized to identify the groups that had statistically significant deviations. The resulting estimates of the ANOVA model is shown in Table 5.1. All statistical analyses were conducted in R 4.0.3 (RCoreTeam, 2021).

## 5.4 RESULTS

### 5.4.1 Species and functional richness over time

Overall, drought had a significant impact on the number of species (Table 5.1). In the first year of treatment, all of the sites had a species richness that was more or less equivalent to one another (Figure 5.1). Nevertheless, in the second year, the study detected a slight decline in species richness from the grazing exclusion (resting) treatment under drought conditions (D+G-), whilst the other treatments appeared to be maintaining a constant species richness. After the second year of treatment, a pattern became apparent: drought treatments, under both grazed (G+) and rested (G-) conditions, experienced a significant loss in species richness, whereas similar treatments (G+ & G-), when conducted under ambient conditions, maintained a relatively higher richness. This pattern persisted from the third observation year (2017) until the final year (2020).

It is interesting that when species richness within the same climatic conditions (i.e. under drought/ambient conditions) was compared, grazed treatments had relatively higher species richness regardless of whether or not there was drought. Again, this phenomenon was observed from the third year until the final. In general, under ambient conditions, species richness fluctuated; it was steady for the first two years, then declined for two years (2017 & 2018). Eventually, the number of species present increased again during the final two years of treatment. However, when drought conditions occurred, the average species richness experienced a decline as the length of the drought increased.

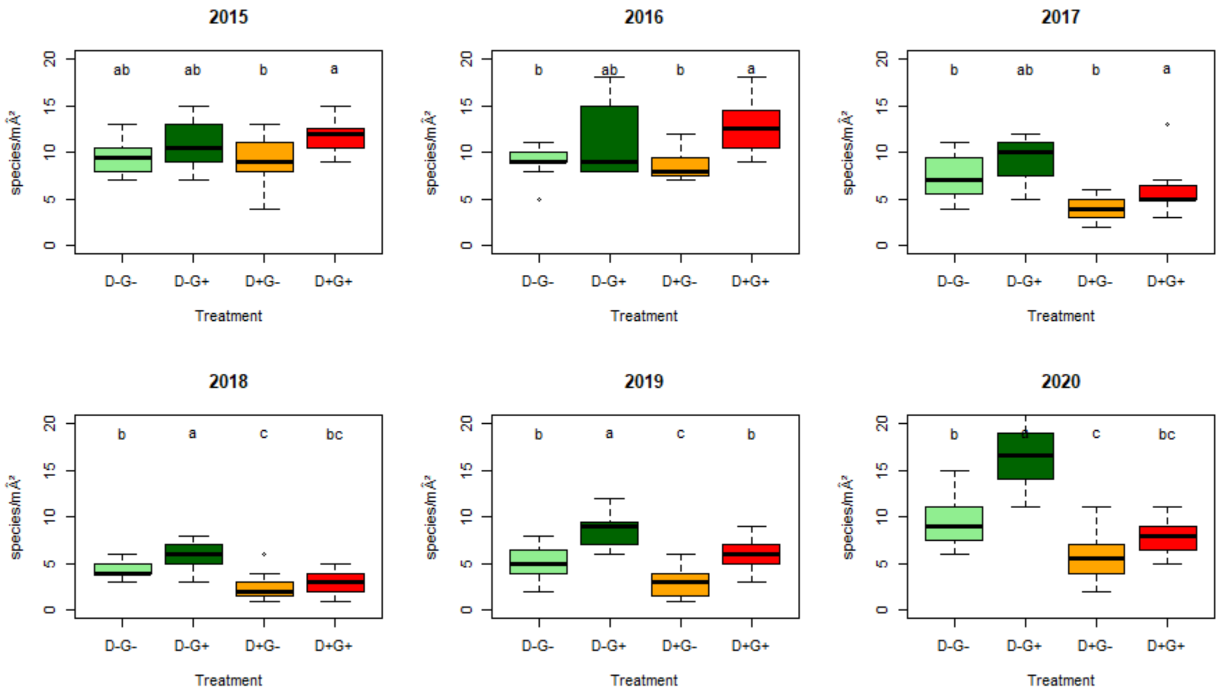


**Figure 5.1** This figure illustrates the impact of drought and grazing treatments on species richness over time.

### 5.4.2 Species accumulation over time

When evaluating the number of species existing in a given location (species richness), one of the most essential factors to consider is how much effort is required to sample the greatest number of species feasible. To demonstrate this point, a species richness curve was constructed. This is a method for the discovery of new species that involves plotting the total number of species discovered against the amount of effort needed to sample those species (i.e. total number of sites). The study found that, initially, the amount of effort and number of species discovered were similar between all studied groups (Figure 5.2). Nonetheless, in the second year, rested treatments (G-) both under drought and ambient conditions, had the lowest number of species per unit area while the other two treatments (D+G+ & D-G+) maintained a relatively high number of species. However, as the experiment progressed, under drought conditions, it took more effort to uncover the same number of species found under normal conditions.

A difference between the drought and non-drought treatments was observed from the third treatment year (2017). The non-drought treatments had 10 species on average at two locations, whereas the drought treatments required six sites to yield the same number of species. Figure 5.2 shows that in general, new species were found at a rapid rate at the beginning, but this rate eventually slowed down to the point where each subsequent new species demands a progressively greater amount of effort to discover. The rate at which this phenomenon happened varied depending on whether or not there was drought. For instance, in 2017, under drought treatments, the species richness curve leveled off at six sites, and after that, sampling more sites provided very little additional benefit. This was the case because, beyond six sites, there was no further increase in species richness.

Under ambient conditions, the asymptote appeared at about ten sites. The study also discovered differences between grazing (G+) and rested (G-) treatments under both drought and non-drought conditions. Throughout the first four years of the study, the rested treatments had more species per unit area, especially under drought conditions; nevertheless, this species richness reduced during the final two years of the study. However, it was only after the first three years that a distinction in species richness per unit area between plots that have been grazed and those that have been let to rest was observed. Interestingly, the greatest difference between drought and non-drought treatments occurred in the fourth year of the study (2018).

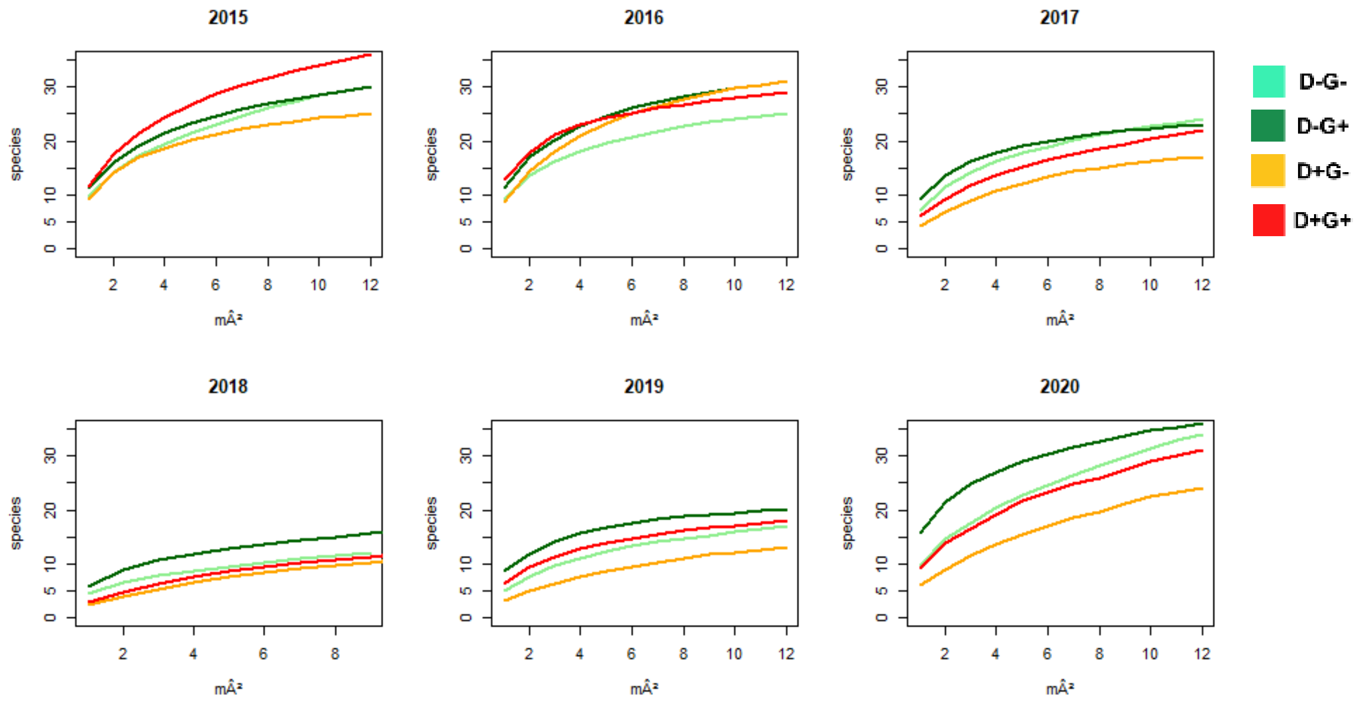


**Figure 5.2** This graph depicts the species diversity curve through time. It represents the rate at which new species are discovered or accumulated. This graph compares the overall number of species to the quantity 1m$^2$-quadrat belonging to the same treatment. The x-axis represents the number of 1m-quadrats (m$^2$).

**Table 5.1** Estimates of the two-way ANOVA model that fitted the effect of drought, grazing and the combined effect of drought and grazing on the species richness

| | | **RICHNESS** | | |
|---|---|---|---|---|
| Year | | Df | F value | Pr(>F) |
| 2015 | Drought | 1 | 0.107 | 0.745 |
| | Grazing | 1 | 9.451 | 0.004 ** |
| | Drought:Grazing | 1 | 0.723 | 0.399 |
| | Residuals | 44 | | |
| 2016 | Drought | 1 | 0.651 | 0.424 |
| | Grazing | 1 | 15.422 | 0.000 *** |
| | Drought:Grazing | 1 | 1.809 | 0.185 |
| | Residuals | 44 | | |
| 2017 | Drought | 1 | 19.986 | 0.000 *** |
| | Grazing | 1 | 9.005 | 0.004 ** |
| | Drought:Grazing | 1 | 0.184 | 0.67024 |
| | Residuals | 44 | | |
| 2018 | Drought | 1 | 39.455 | 0.000 *** |
| | Grazing | 1 | 6.171 | 0.017 * |
| | Drought:Grazing | 1 | 1.936 | 0.1716 |

|  |  |  |  |  |
|---|---|---|---|---|
|  | Residuals | 41 |  |  |
| 2019 | Drought | 1 | 18.203 | 0.000*** |
|  | Grazing | 1 | 43.084 | 0.000 *** |
|  | Drought:Grazing | 1 | 0.027 | 0.870 |
|  | Residuals | 44 |  |  |
| 2020 | Drought | 1 | 32.012 | 0.000*** |
|  | Grazing | 1 | 26.535 | 0.000 *** |
|  | Drought:Grazing | 1 | 3.452 | 0.0699 |
|  | Residuals | 44 |  |  |

Significance codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

**Table 5.2** Estimates of the two-way ANOVA model that fitted the effect of drought, grazing and the combined effect of drought and grazing on the Shannon Weiner index

|  |  | SHANNON |  |  |
|---|---|---|---|---|
| Year |  | Df | F value | Pr(>F) |
| 2015 | Drought | 1 | 0.053 | 0.819 |
|  | Grazing | 1 | 4.963 | 0.031* |
|  | Drought:Grazing | 1 | 1.222 | 0.274 |
|  | Residuals | 44 |  |  |
| 2016 | Drought | 1 | 0.006 | 0.940 |
|  | Grazing | 1 | 0.202 | 0.655 |
|  | Drought:Grazing | 1 | 0.584 | 0.449 |
|  | Residuals | 44 |  |  |
| 2017 | Drought | 1 | 11.246 | 0.002** |
|  | Grazing | 1 | 2.312 | 0.135 |
|  | Drought:Grazing | 1 | 0.585 | 0.448 |
|  | Residuals | 44 |  |  |
| 2018 | Drought | 1 | 13.797 | 0.000*** |
|  | Grazing | 1 | 2.328 | 0.135 |
|  | Drought:Grazing | 1 | 0.237 | 0.629 |
|  | Residuals | 41 |  |  |
| 2019 | Drought | 1 | 6.736 | 0.013* |
|  | Grazing | 1 | 20.391 | 0.000*** |
|  | Drought:Grazing | 1 | 1.281 | 0.264 |
|  | Residuals | 44 |  |  |
| 2020 | Drought | 1 | 4.203 | 0.046* |
|  | Grazing | 1 | 22.979 | 0.000*** |
|  | Drought:Grazing | 1 | 0.841 | 0.364 |
|  | Residuals | 44 |  |  |

Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

**Table 5.3** Estimates of the two-way ANOVA model that fitted the effect of drought, grazing and the combined effect of drought and grazing on the species' evenness (EVENNESS).

| | | EVENNES | | |
|---|---|---|---|---|
| | | Df | F value | Pr(>F) |
| 2015 | Drought | 1 | 0.376 | 0.543 |
| | Grazing | 1 | 2.43 | 0.126 |
| | Drought:Grazing | 1 | 1.052 | 0.311 |
| | Residuals | 44 | | |
| 2016 | Drought | 1 | 0.101 | 0.753 |
| | Grazing | 1 | 4.677 | 0.036* |
| | Drought:Grazing | 1 | 0.063 | 0.803 |
| | Residuals | 44 | | |
| 2017 | Drought | 1 | 1.129 | 0.294 |
| | Grazing | 1 | 2.294 | 0.137 |
| | Drought:Grazing | 1 | 0.035 | 0.853 |
| | Residuals | 44 | | |
| 2018 | Drought | 1 | 4.928 | 0.033* |
| | Grazing | 1 | 0.008 | 0.9277 |
| | Drought:Grazing | 1 | 3.198 | 0.0821 |
| | Residuals | 36 | | |
| 2019 | Drought | 1 | 2.097 | 0.155 |
| | Grazing | 1 | 0.411 | 0.525 |
| | Drought:Grazing | 1 | 0.129 | 0.721 |
| | Residuals | 41 | | |
| 2020 | Drought | 1 | 39.529 | 0.000*** |
| | Grazing | 1 | 2.271 | 0.139 |
| | Drought:Grazing | 1 | 3.252 | 0.0782 |
| | Residuals | 44 | | |

Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

### 5.4.3 Shannon diversity index over time

First and foremost, initial levels of diversity were comparable across all treatments (Figure 5.3). It took some time before the effect of the treatment became apparent because, even after two years, there were only slight variations in species diversity between the different treatments. Differences between treatments were only discernible in the third year, which coincided with a decline in total diversity. However, the diversity in both drought treatments (D+G+ and D+G-) dropped to a level that was lower than that of the non-drought treatments (D-). It would appear at this stage that there was no discernible difference in diversity between the treatments that were carried out under identical climatic conditions. It was not until the fourth treatment year, 2018, that differences in diversity between groups under similar climatic settings were identified. Generally, in both drought and non-drought settings, grazed treatments (G+) had a tendency of greater diversity of plant species than rested treatments (G-). Overall, the treatment that served as a control (D-G+) had the highest diversity, but the effect of long-term resting under drought conditions yielded the least amount of diversity.

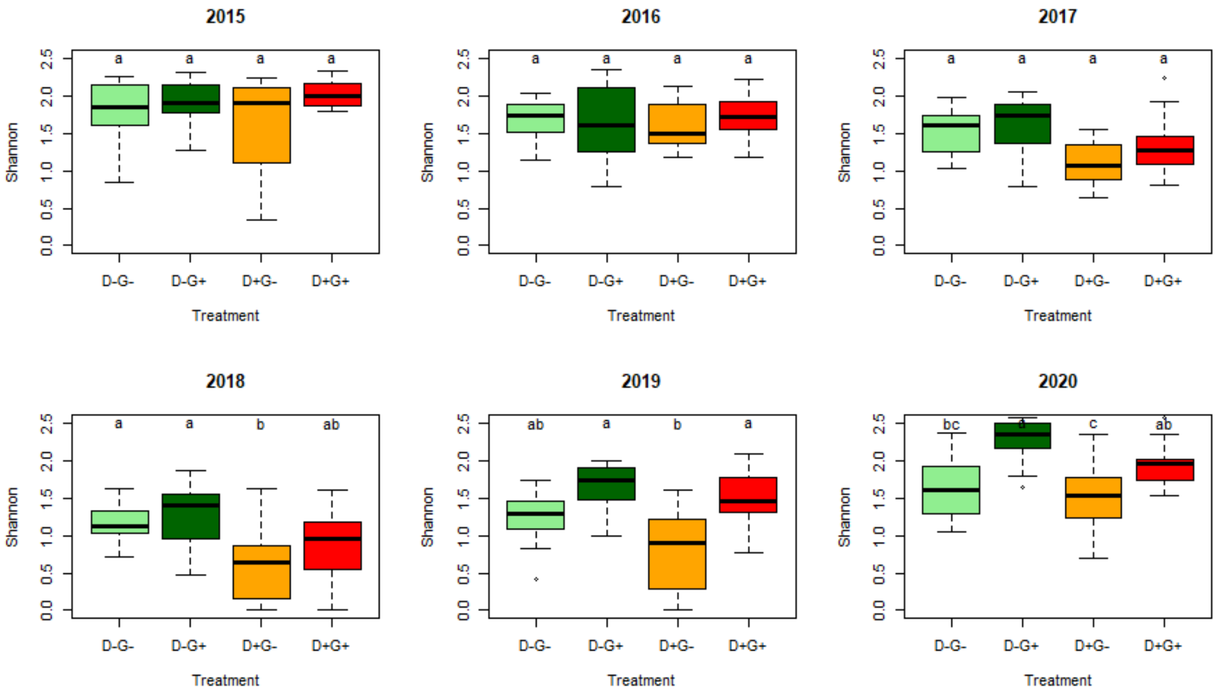


**Figure 5.3** This graph examines the Shannon-Wiener Index-based diversity of the different treatments over time.

### 5.4.4 Species evenness over time

Drought treatments, over time, had higher species evenness than non-drought treatments (Figure 5.4). However, in the first three years of the experiment (2015 – 2017), although not significant, treatments that were rested (G-) had higher species evenness than treatments that had been grazed, regardless of whether or not there was a drought. Interestingly, in the fourth and fifth years of the experiment, there was little convergence in species evenness among the different treatments. Finally, in the last experimental year, non-drought treatments had a relatively lower species evenness than drought treatments. Generally, there were minimal differences in species evenness between treatments under similar climatic conditions (i.e. D-G- vs. D-G+ & D+G+ vs. D+G-).

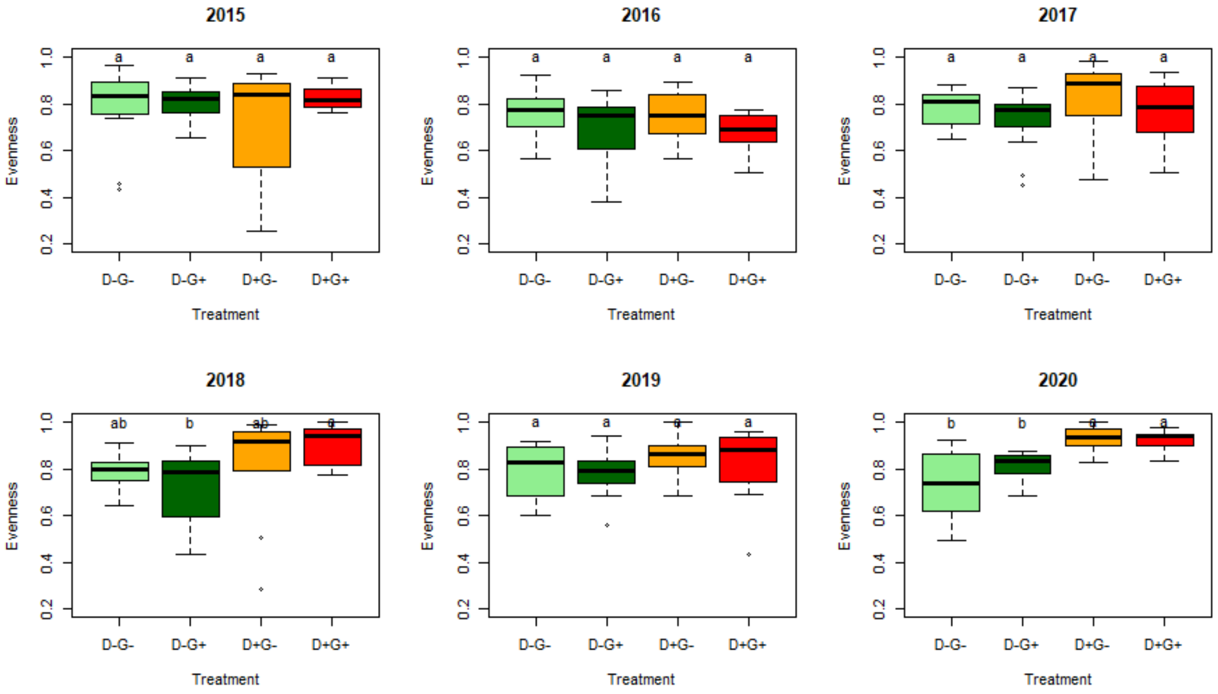


**Figure 5.4** This figure shows a comparison of species evenness of different treatments over a period of six years at the DroughtAct experiment.

### 5.4.5 Effects of treatment on diversity shift

The study indicated that there was not much of a difference in the species diversity between the treatments at the beginning of the experiment (Figure 5.5). However, after a total of six years of the experiment, there was a clear and discernible gap in performance between the treatments. It is interesting to note that treatments that were subjected to the same climatic conditions, such as those that were subjected to drought and those that were subjected to ambient conditions, tended to be more similar to one another in terms of diversity than treatments that were subjected to different climatic conditions (i.e. D- vs. D+). However, drought treatments were more comparable to one another than treatments conducted under normal conditions. In conclusion, drought treatments (D+) had the greatest diversity changes. Moreover, under drought conditions, rested plots (G-) experienced a greater decline in diversity than grazed plots (G+).

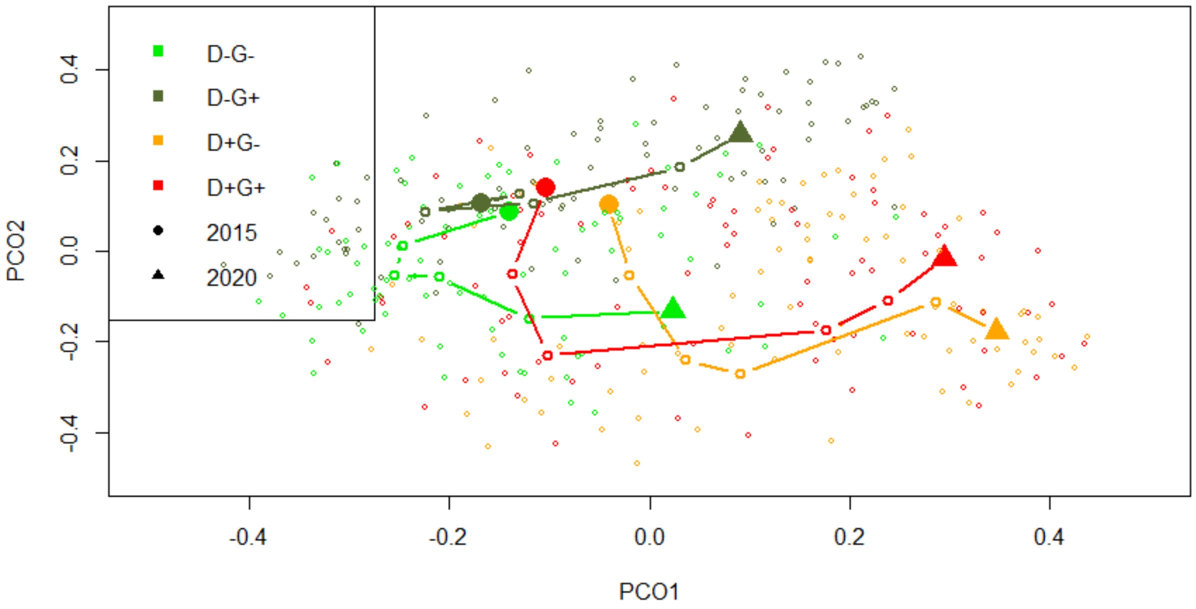


**Figure 5.5** This graph compares treatment differences within and between years. The circles indicate the first year of treatment, while the triangles represent the last year. The lines follow the centroids for each treatment and year, while the small open circles represent an individual sampling quadrat in the color of the respective treatment.

### 5.4.6 Effect of long-term drought and grazing on functional diversity

In the first year of the study, the analysis suggests that functional richness, evenness, and divergence were similar across treatments. In the final year of the study, however, there is a discernible difference across treatments; grazed treatments appear to have greater functional richness than non-grazed treatments, regardless of drought conditions. Furthermore, grazed and non-grazed treatments under ambient conditions had relatively higher functional richness than under drought conditions. Nevertheless, non-grazed treatments (G-), both under drought and non-drought conditions, had slightly higher functional evenness than grazed treatments (G+). Moreover, the combination of drought and resting (D+G-) resulted in the highest functional evenness, followed by rested treatment under ambient conditions (D-G-). Interestingly, both these treatments had the highest functional divergence in the final year. However, the non-grazed treatment under drought conditions (D+G-) had a slightly higher divergence than under ambient conditions.

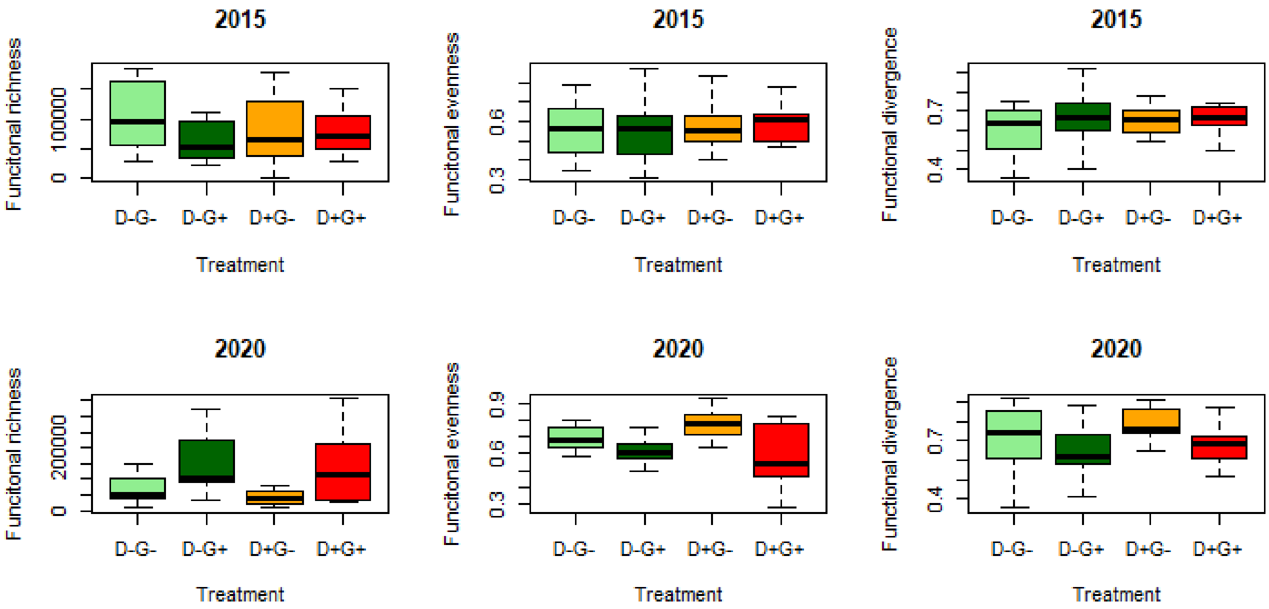


**Figure 5.6** This figure illustrates functional richness, evenness and divergence between the first year of the study (2015) and the final year (2020), comparing the different treatments.

## 5.5 DISCUSSION

The primary findings from this study are that extended periods of drought and resting (grazing exclusion) have a cumulatively detrimental effect on taxonomic diversity, resulting in lower species richness as well as a lower number of species present per unit of land area. However, although, functional richness was negatively affected by resting, functional evenness and divergence appeared to have profited from it.

The first hypothesis that was tested in the investigation was that drought would, in the long run, cause a reduction in the amount of functional and taxonomic diversity, particularly as a consequence of the interaction between the effects of drought and grazing (H1). This hypothesis can be proven to be true because all of the drought treatments (D+) exhibited a general decrease in species diversity and functional richness. However, the results showed that the greatest diversity losses were caused by a combination of drought and resting (grazing exclusion). In addition, the research showed that both functional and taxonomic richness was often higher in grazed treatments, independent of whether or not there was a drought. This could be explained by the self-shading effect that occurs after long-term resting. Also, grazing creates gaps and opportunities for other species to grow by reducing the biomass of more competitive species. Similar findings have been reported in other studies; according to a study conducted by Mudongo et al. (in prep.), long-term resting has a considerable negative effect on vegetation, especially under drought conditions. This is because resting-related self-shading and drought-related tiller mortality have interactive effects that ultimately result in the loss of tufts, leading to rangeland degradation.

The observed decline in species richness due to drought has been reported in other studies, Wang et al. (2021b) found that competitive species with high biomass production generally have low drought resistance. Moreover, such risk-prone species are predicted to impair the drought resistance of communities (Wang et al., 2021a). In the previous chapter, which focused on winner and loser species and functional types, and it was discovered that generally, competitive functional groups such as broad-leaved perennial grasses and very-broad-leaved perennial grasses were the greatest losers of long-term drought. The establishment of links between plant functional types that are winners and losers of drought and taxonomic diversity enables us to better understand the dynamics of vegetation in the face of changing climate. Elst et al. (2017)'s findings provide evidence in support of this contention. The authors discovered that in order to comprehend how communities respond to climatic extremes, one must concentrate their attention not only on the characteristics of individual species but also on the relationships between species (richness).

The observed relationship between species richness and drought reveals an important puzzle which moves us closer to understanding the impact of drought on overall taxonomic diversity in dryland grasslands. Brown et al. (2007) also reported that the small-scale species richness might reveal useful information about an ecosystem. Because of this, having a solid understanding of the factors that have an impact on species richness is particularly vital for implementing the concept of biodiversity conservation into practice. In addition, the results of a study by Kennedy et al. (2003) suggest that sites with a greater variety of species are more prone to change than those with a lower variety of species. Drought resulted in species-rich grassland sites experiencing greater declines in grass abundance and standing crops than species-poor grassland sites. In contrast to these findings, the DroughtAct experiment discovered that experimental units with a greater variety of species such as D+G+ treatments were more resistant to the impacts of drought than experimental units with a lower variety of species such as D+G- treatments. A more recent study conducted by Sintayehu (2018) supports these findings; the study reports that biodiversity stabilizes ecosystem productivity and probably productivity-dependent ecosystem services during both moderate and extreme climate events.

It was hypothesized that the longer the drought period lasts, the greater the differences will be between treatments or different growth seasons (H2). This hypothesis can be confirmed. From the principal coordinate analysis, it was shown that all treatments exhibited similar species composition at the beginning of the experiment. Furthermore, functional richness, evenness and divergence were similar across treatments in the first year. However, as the length of the drought continued, a growing number of differences were observed, not only between the treatments but also between the various growth periods. The overall number of species per unit area had a steeper fall during drought conditions compared to ambient conditions; this pattern became more obvious as the length of the drought continued. It appeared that drought had a detrimental effect on the number of species per unit area. This is not an uncommon result. Kennedy et al. (2003) found that at the peak of drought, the average species diversity declined by 12.7% and the standing crop by 38.1%. The abundance of grass decreased to 87.5% of what it had been before the drought.

Functional richness was greatly negatively impacted by long-term drought and resting. Similar to species richness, the observed decline in functional richness can be explained by a long-term build-up of moribund material under rested plots, resulting in detrimental self-shading which in turn causes mortality of the shaded species. The chapter on winners and losers indicated that, to some extent, the winners of long-term drought and resting were narrow-leaved perennial grasses and forbs, suggesting that functional services offered by the broad-leaved and very-broad-leaved perennial grasses would greatly diminish under drought and rested treatments. In a similar vein, Dovrat et al. (2021) discovered that functional richness was positively correlated with species richness, and that lost taxa were often large or drought-intolerant species with poor functional plasticity. In addition, this study found that under somewhat dry conditions, species richness was low, and increased aridity led to a greater decline in functional richness than in species richness.

The great functional evenness and divergence under drought treatments as well as rested treatments strongly suggest that the species observed in both treatments have differentiated into various niches. In addition, as the length of the drought period extended, the dominating competitive species experience a significant reduction, which resulted in a greater degree of functional evenness. Moreover, the mortality of abundant species results in the relief of competitive pressure, which in turn leads to the introduction of new species that may occupy other niches and make greater use of the available resources. This is not uncommon, a study by Thonicke et al. (2020) showed that functional diversity resulted from environmental and competitive filtering. The high functional divergence occurred as a direct consequence of drought which limited tree growth, and made niche differentiation more important.

In conclusion, the study postulated that the optimal conditions for the greatest amounts of functional and taxonomic diversity would be reached when drought and grazing impacts were moderate (H3). The four treatments in the study; grazing under ambient conditions (D-G+), grazing exclusion under ambient conditions (D-G-), grazing exclusion under drought (D+G-), and grazing under drought conditions (D+G+) represented different levels of disturbance (grazing) and stress (drought). Under all grazing exclusion plots (G-), disturbance was extremely minimal whereas, under all grazed plots (G+), drought (D+G+) may exacerbate the impact of the disturbance. However, grazing under ambient conditions (D-G+), which was the control treatment, may arguably represent moderate disturbance circumstances. Therefore, as this treatment, at the end of the study, had the highest functional and taxonomic richness, the number of species per unit area and the highest diversity (Shannon), the third hypothesis can be confirmed to be true. These findings are in line with the intermediate disturbance hypothesis (IDH) which suggests that local species diversity is maximized when an ecological disturbance is neither too rare nor too frequent (Connell, 1978).

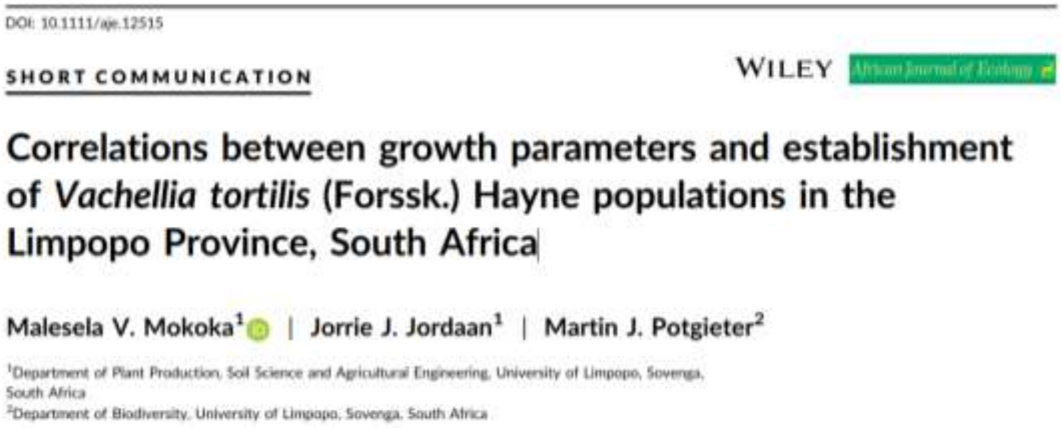
## 5.6 CONCLUSIONS

According to the findings of this study, long-term drought has a negative impact on functional and taxonomic diversity, as shown by a lower number of species per unit area, functional richness and a lower richness of species under drought plots. In addition, although the combination of drought and grazing was anticipated to result in the highest diversity losses, the study revealed that under drought conditions, extended periods of resting had a greater negative influence on diversity than grazing did. To gain a better knowledge of vegetation dynamics, particularly diversity-related mechanisms, it is critical to research diversity indices such as species richness in connection to functional traits. This is because it tells a more complete story than investigating traits or diversity alone. Not only may functional and taxonomic diversity, and particularly species richness, be used to indicate the health of an ecosystem, but it can also be used to inform conservation policy.

The study recommends that more experiments involving the manipulation of precipitation be carried out, as these types of experiments are uniquely capacitated to investigate the impact of multiple drivers of an ecosystem function simultaneously, particularly in dryland grasslands. This will enable greater joint work in dryland grasslands, which are expected to face more climate extremes such as drought in the future. In the following chapter, an investigation is conducted into the influence that bottom-up mechanisms, such as soil type, and top-down mechanisms, such as precipitation, have on the establishment and recruitment of invading woody species in dryland grasslands in the province of Limpopo.

To determine the factors affecting tree populations, the next chapter investigates the correlations between the growth parameters and establishment of *Vachellia tortilis* (Forssk.) Hayne populations in Limpopo province.

# CHAPTER 6: CORRELATIONS BETWEEN GROWTH PARAMETERS AND ESTABLISHMENT OF VACHELLIA TORTILIS (FORSSK.) HAYNE POPULATIONS IN THE LIMPOPO PROVINCE, SOUTH AFRICA



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SHORT COMMUNICATION

WILEY African Journal of Ecology

Correlations between growth parameters and establishment of *Vachellia tortilis* (Forssk.) Hayne populations in the Limpopo Province, South Africa

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**Note:** This chapter addresses the second part of the second objective "*Determine the factors affecting tree populations, particularly tree establishment patterns.*"

## 6.1 ABSTRACT

It has been documented that bush encroachment is detrimental to savanna ecosystems globally because it impacts grazing capacity, livestock management, and the livelihoods of communities that are dependent on ecosystem services from this biome. *Vachellia tortilis* (Forssk.) Hayne is an indicator of bush encroachment in South Africa, but little is known of the influence of climatic and environmental factors, particularly rainfall and soil on its establishment. Thus, this study set out to investigate a selected number of parameters (tree density, tree height, growth rings, crown diameter and stem circumference – measured at breast height) related to the growth and establishment of *V. tortilis* populations, as affected by both rainfall and soil type. This was done by examining two natural populations in Mankweng and Bela-Bela in the Limpopo Province of South Africa, which have different rainfall and soil conditions. Results indicated that the growth of *V. tortilis* is significantly affected by both rainfall and soil type, with the tree height being considerably influenced by rainfall, but not so by soil type. Both rainfall and soil type did not have a substantial effect on the number of growth rings. Crown diameter was affected by soil type, but rainfall did not prove to have the same effect. Based on the tree density survey, a prediction model was created using the relationship between stem size and tree rings. However, the absence of a correlation between rainfall and establishment strongly suggests that rainfall cannot be used, on its own, to determine the establishment sequence and the pattern establishment. The study suggests that natural developments responsible for establishment patterns and population dynamics of woody species are complex, and their effects are only apparent after an extensive period. Therefore, to understand these influential processes comprehensively, several seasons of observations and monitoring are recommended.

**Key words**: Bush encroachment, dendrochronology, growth rings, population establishment, population growth, savanna

## 6.2 INTRODUCTION

Growth rings are the concentric circles visible in tree-trunk cross sections. They provide records of ecosystem events like fire, insect outbreaks and logging. Meteorological conditions have a substantial effect on the formation of growth rings. Under optimum growth conditions (warm temperature and regular rainfall), the rings that are formed will be wider than those in a colder year, or one with extensive water shortages (Fritts, 1966). Growth rings have proven to be an invaluable resource for age determination in woody plants(Bowman et al., 2013). Climate has been employed as a source of explanations for the condition of tree rings, as well as a prediction for future tree-ring growth. Equally tree rings have been used to reveal several features of past climate (Hughes, 2002).

Tree growth form may have a positive or negative effect on the growth of grass, which in turn, will affect tree establishment and growth. Due to the higher organic carbon content in the soil, bulk density is often lower in soil under tree canopies (Smith and Goodman, 1986). Furthermore, Smit (2004) found that there is a significant increase in both stem diameter and shoot extension of *Vachellia nilotica* trees whose neighbours had been removed within a radius of 5 m.

*Vachellia tortilis* (Forssk.) Hayne subsp. *heteracantha* (Burch.) Brenan (previously *Acacia tortilis* subsp. *heteracantha*) is a distinctive African tree. The species belongs to the family Fabaceae (Mimosoideae). Its distribution and habitat are widespread throughout the savanna biome and dry zones of Africa, from Senegal to Somalia and southwards to South Africa (Hegazy and Elhag, 2006). It is morphologically variable, and can be multi-stemmed shrubs (ssp. *tortilis*), or single-stemmed trees, up to 20 m tall, with rounded (ssp. *raddiana*) or flat-topped (ssp. *heteracantha* and *spirocarpa*) crowns. It is a slow-growing dryland species, with deep rooting habits and a spreading umbrella-shaped crown (Council, 2002).

*Vachellia tortilis* and various other *Vachellia* species are categorized as species that indicate bush encroachment in South Africa (Nel et al., 2004). Using *V. tortillis* as an example, it is critical to study the growth and development of these species, to have a clearer understanding of their growth determinants and ultimately the causes of their encroachment. The study thus investigated the relationship between two growth determinants of *V. tortilis*, namely; rainfall and soil type, on a select number of growth parameters, at two sites in the Limpopo Bushveld, South Africa.

## 6.3 MATERIALS & METHODS

### 6.3.1 Study region

The research was conducted in the Capricorn and Waterberg districts of the Limpopo Province, at two locations (150 km apart), namely; the University of Limpopo's Syferkuil Experimental Farm (Capricorn district) and the Sondela Nature Reserve (Waterberg district). Three experimental sites were involved; two at Syferkuil and one at Sondela. Two experimental sites at Syferkuil (Site 1 and Site 2) were used to study growth ring formation of *V. tortilis* on different soil types at the same mean annual rainfall. Two sites, one at Syferkuil and one at Sondela (Site 1 and Site 3), were used to study growth ring formation of *V. tortilis* on a similar soil type at different mean annual rainfalls.

The Syferkuil Experimental Farm (Syferkuil) is situated near Mankweng (23°49' S; 29°41' E) in the Pietersburg Plateau False Grassveld (Acocks, 1998). The mean temperature at Syferkuil ranges between 28 and 30°C, and the average long-term annual rainfall is 450 mm per annum. The dominant grasses are typical bushveld grasses, such as *Aristida* species, *Heteropogon contortus* and *Themeda triandra*, while the woody component is dominated by *Vachellia* species, such as *V. habeclada* and *V. rehmanniana*. Following the South African soil classification system, two soil types were identified: Glenrosa and Hutton soils. This categorization assigns soil forms based on distinct combinations of topsoil and subsoil horizons (layers). Other properties of the soil form are then used to define the soil series. Please see Group and Macvicar (1991) for further details on this classification system. The particle size distribution of the soil was determined using the sieve and pipette method, and the soil texture classification was based on the United States Department of Agriculture (USDA) classification.

**Table 6.1** Soil chemical properties of Glenrosa and Hutton soils.

| Soil Type | P mg/kg | K mg/kg | Ca mg/kg | Mg mg/kg | Exch. Acidity cmol/L | Total cations cmol/L | pH (KCl) | Zn mg/kg | Mn mg/kg | Cu mg/kg | Org. C % | N % | Clay % |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Glenrosa | 1.88 | 241.88 | 159.38 | 64.38 | 0.04 | 3.15 | 4.77 | 0.5 | 10.63 | 1.63 | 2 | 0.17 | 19 |
| Hutton | 0.64 | 83.97 | 187.18 | 114.74 | 0.05 | 3.32 | 4.35 | 0.19 | 13.46 | 2.5 | 1.6 | 0.12 | 23 |

The Sondela Nature Reserve (Sondela; Site 3) is situated on the southern part of the Springbok flats, near the town of Bela-Bela (28°21'E, 24°25'S). The long-term average annual rainfall of this site is 630 mm. The long-term daily average maximum and minimum temperatures vary between 29.7°C and 16.5°C for December and 20.8°C and 3.0°C for July (1994 – 2020), respectively. The vegetation type is classified as Sourish Mixed Bushveld (Acocks, 1998) or, according to (Low and Rebelo, 1998), Mixed Bushveld. The woody layer is dominated by *Vachellia* species and *Dichrostachys cinerea*, and the grass layer by *Eragrostis* species (*E. barbinodis* and *E. rigidior*), *H. contortus*, *Panicum maximum* and *T. triandra*. The soil of the study area is of the Hutton form (Stella family) (Group and Macvicar, 1991).

### 6.3.2 Data collection

Fifty *V. tortilis* trees were selected at each site. These individuals were represented by five height classes, namely 0.0 – 0.5 m (representing seedlings/young trees), >0.5 – 1.5 m, 1.5 – 2.0 m, >2.0 – 3.0 m and >3.0 m. Each class included 10 trees. The canopy diameter of each tree in the different height classes was also determined, using the line intercept method (Canfield, 1941) whereby the distance covered by a canopy that intercepts the tape measure, regardless of whether the stem of the tree is within the 2.0 m parameter, is recorded and computed. The tree height and crown diameter were measured using a measuring tape. The selected plants were then felled, using a chainsaw.

A sample of the stem of each plant was used to determine the number of year rings. Stem samples of 500 mm long were cut. Discs of 200 mm width (to prevent cracking) were sectioned from the samples and sanded at the University of the Limpopo's Technical Section, using a belt sander and a series of belts between 60 and 120-grain size. Growth rings were counted using an Olympus SZ30 dissecting microscope with an eye piece graticule. Rings were counted in a Y pattern emanating from the center of the stem. Every 10th year was marked with a pinprick, adapted from the method used by (Stokes and Smiley, 1996). At branch entry points the rings are scalloped. These areas were not used for counting the rings or measuring the stem diameter. The three lineage counts per stem were averaged and where necessary, adaptations were made to compensate for fungal infected areas. Where growth rings were not clearly visible or where holes occurred in the trunks, the number of rings that occurred in unaffected heartwood was divided by the length of the affected area and equaled the years approximated to that area (Mushove et al., 1995).

### 6.3.3 Data analysis

Data were analyzed using GenStat® (Payne et al., 2011). To determine the differences in tree characteristics (tree heights, number of growth rings, canopy diameter and stem circumference), data were subjected to a two-tailed T test for independent samples. To determine the relationships between tree heights, stem circumference, canopy diameter and the number of growth rings, tree characteristic data were totaled and subjected to multiple regression analyses (Draper and Smith, 1998). Regressions that were obtained relating to meteorological factors (rainfall and soil) and growth rings (tree age) were compared, using Pearson's correlation coefficient.

## 6.4 RESULTS AND DISCUSSION

Where stem circumference of *V. tortilis* on the Hutton and Glenrosa soil types is concerned (Site 1 and Site 2), insignificant differences ($p > .05$) occurred in two of the height classes, namely; the >0.0–0.5 m (1 cm difference) and the >2.0–3.0 m height class (4.6 cm difference) (Table 6.1). Stem circumferences in the other three height classes differed significantly ($p < .05$,). No significant differences in tree height, for any of the height classes, occurred between the two sites (Table 6.1). In four of the five height classes, differences in crown diameter between sites were significant ($p < .05$), namely in the >0.0–0.5 m (36.5 cm difference), >0.5–1.5 m (132.1 cm difference) >1.5–2.0 m (206.9 cm difference) and >3 m height classes (73.2 cm difference). The only insignificant difference occurred in the >2.0–3.0 m height class (37.2 cm difference) (Table 6.1). Where the number of growth rings is concerned, significant differences ($p < .001$) occurred in two of the height classes (Table 6.1), namely; the >0.0–0.5 m (14 rings difference) and the >3.0 m height class (32 rings difference).

Where stem circumference at the two sites that differed in rainfall is concerned (Site 1 and Site 3), significant differences ($p < .001$) occurred in only two of the height classes, namely in the >0.5–1.5 m (11.1 cm difference) and the >1.5–2.0 m height class (12.8 cm difference) (Table 6.1). In two instances, insignificant differences ($p > .05$) occurred in tree height, namely; in the >0.5–1.5 m (9 cm difference) and the >2.0–3.0 m height class (2 cm difference). Tree height in the other three height classes differed significantly ($p < .05$, Table 6.1). Only two crown diameter groups differed significantly ($p < .05$), namely; the >2.0–3.0 m (159.2 cm difference) and the >3.0 m (267.9 cm difference). Similarly, in only two of the height classes, differences in growth rings between sites were significant ($p < .05$), namely; in the >0.5–1.5 m (11 rings), >1.5–2.0 m (21 rings) and >3 m height class (20 rings).

In general, soil type affected tree rings, crown diameter and stem circumference. Although, the effect of soil type was significant on crown diameter and stem circumference, it was, however, insignificant on tree rings. While tree height and tree rings were affected by rainfall, only tree height was significantly influenced. Upon speculation, keeping the physical properties, especially the water holding capacity, of the specific soil type in mind, the difference in annual rainfall was apparently not large enough to allow soil water to be a limiting factor between the two sites where both crown diameter and stem circumference were concerned.

As indicated in Table 6.2, various plant growth parameters were highly correlated with each other ($p < .01$). There was a significant relationship ($p < .01$) between the number of growth rings and stem circumference ($r^2 = .98$), tree height ($r^2 = .85$) and a lower, but significant relationship with crown diameter ($r^2 = .69$). Stem circumference gave the highest correlation with the number of growth rings ($r^2 = .98$), compared to other growth parameters that were included in the study. There was also a significant ($p < .01$) relationship between stem circumference and tree height ($r^2 = .66$). Similarly, there was also a significant relationship between stem circumference and crown diameter ($r^2 = .87$). Tree height and crown diameter were also significantly ($p < .01$) correlated ($r^2 = .62$).

**Table 6.2** Statistical analysis for the effects of rainfall and soil type on *Vachellia tortilis* growth parameters.

| | Tree characteristic | Height class (m) | Mean (m) | P-value |
|---|---|---|---|---|
| Site 1 vs Site 2 | Stem circumference | >0.10 – 0.50 m | 1.000 ± 0.750 | 0.201 |
| (Similar rainfall) | | 0.50 – 1.50 m | 10.800 ± 1.190 | <0.001** |
| | | 1.50 – 2.00 m | 4.700 ± 1.980 | 0.029* |
| | | 2.10 – 3.00 m | 4.600 ± 3.780 | 0.239 |
| | | >3.00 m | 15.000 ± 3.670 | <0.001** |
| | Tree height | >0.10 – 0.50 m | 0.010 ± 0.030 | 0.611 |
| | | 0.50 – 1.50 m | 0.040 ± 0.120 | 0.707 |
| | | 1.50 – 2.00 m | 0.030 ± 0.060 | 0.606 |
| | | 2.10 – 3.00 m | 0.160 ± 0.130 | 0.221 |
| | | >3.00 m | 0.220 ± 0.220 | 0.333 |
| | Crown diameter | >0.10 – 0.50 m | 0.370 ± 0.110 | 0.006** |
| | | 0.50 – 1.50 m | 1.320 ± 0.350 | 0.002** |
| | | 1.50 – 2.00 m | 2.070 ± 0.230 | <0.001** |
| | | 2.10 – 3.00 m | 0.170 ± 0.350 | 0.630 |

| | | | | |
|---|---|---|---|---|
| | | >3.00 m | 0.730 ± 0.260 | 0.556 |
| | Number of growth rings | >0.10 – 0.50 m | 1.70 ± 0.980 | 0.099* |
| | | 0.50 – 1.50 m | 12.900± 0.980 | <0.001** |
| | | 1.50 – 2.00 m | 10.700 ± 5.870 | 0.093 |
| | | 2.10 – 3.00 m | 7.300 ± 9.040 | 0.430 |
| | | >3.00 m | 31.200 ± 7.940 | <0.001** |
| Site 1 vs Site 3<br>(Similar soil types) | Stem circumference | >0.10 – 0.50 m | 0.400 ± 0.670 | 0.556 |
| | | 0.50 – 1.50 m | 11.100 ± 1.400 | <0.001** |
| | | 1.50 – 2.00 m | 12.800 ± 2.600 | <0.001** |
| | | 2.10 – 3.00 m | 2.800 ± 3.920 | 0.484 |
| | | >3.00 m | 1.200 ± 5.980 | 0.843 |
| | Tree height | >0.10 – 0.50 m | 0.009 ± 0.025 | 0.0727 |
| | | 0.50 – 1.50 m | 0.274 ± 0.078 | 0.006** |
| | | 1.50 – 2.00 m | 0.120 ± 0.049 | 0.024* |
| | | 2.10 – 3.00 m | 0.002 ± 0.118 | 0.987 |
| | | >3.00 m | 0.992 ± 0.372 | 0.019* |
| | Crown diameter | >0.10 – 0.50 m | 0.180 ± 0.120 | 0.132 |
| | | 0.50 – 1.50 m | 0.040 ± 0.230 | 0.870 |
| | | 1.50 – 2.00 m | 0.260 ± 0.350 | 0.467 |
| | | 2.10 – 3.00 m | 1.590 ± 0.500 | 0.008** |
| | | >3.00 m | 2.680 ± 0.740 | 0.005** |
| | Number of growth rings | >0.10 – 0.50 m | 1.500 ± 1.040 | 0.167 |
| | | 0.50 – 1.50 m | 11.100 ± 2.120 | <0.001** |
| | | 1.50 – 2.00 m | 21.000 ± 6.390 | 0.004** |
| | | 2.10 – 3.00 m | 10.300 ± 6.770 | 0.146 |
| | | >3.00 m | 20.100 ± 9.600 | 0.059 |

** = Significant at P = 0.05*

*** = Highly significant at P = 0.01*

When data were initially analyzed using linear regression modelling, a highly significant relationship between the stem circumference and the number of growth rings occurred ($p < .001$; $r^2 = .941$). However, there was evidence of nonlinearity, which then was added to the regression model to improve the predictions of the number of rings per site, using quadratic modelling. The end product was a highly significant ($p < .001$) quadratic relationship ($r^2 = .98$; Figure 6.1).

The Pearson's correlation coefficient indicated significant differences between models from the three different sites (both linear and quadratic; Table 6.3). Site 1 appeared to have a linear relationship during young growth (up to 7 cm stem circumference), after which it changed to nonlinear. Relationships at Site 3 appeared to be linear throughout (Pearson's coefficient of correlation = 0), whereas relationships at Site 2 appeared to be nonlinear (Figure 6.1). Subsequently, the equations to estimate the number of growth rings were as follows:

Site 1: $Y = 1.019 + 1.5757xSC – 0.00042SC^2 – 0.3337SC + 0.01102SC^2$

Site 2: $Y = 1.019 + 1.5757xSC – 0.00042SC^2 – 0.548SC + 0.02074SC^2$

Site 3: $Y = 1.019 + 1.5757xSC – 0.00042SC^2$

where: Y, the number of growth rings; SC, stem circumference (cm).

Many studies have explored the relationship between growth rate and wood properties, such as density. Commonly, these studies use diameter at a given tree age to indicate growth rate (Downes et al., 1999). This study indicated that there is a direct, positive relationship between stem circumference and the number of growth rings, and that tree age can be determined, based solely on stem circumference. As a second alternative, the relationship between tree height and the number of growth rings can also be used (Table 6.4).

As living organisms grow in an uncontrolled environment, trees respond to numerous natural growth modifying influences that are both beneficial and detrimental to annual ring formation (Cook, 1987). These factors represent the depth and level of influence that can be exerted by a variety of external factors. The presence of this variability makes the identification of a particular disturbance, such as anthropization, very difficult and uncertain. Furthermore, because this study did not measure the size of the tree rings, determining the influence of external factors on the formation of tree rings becomes difficult.

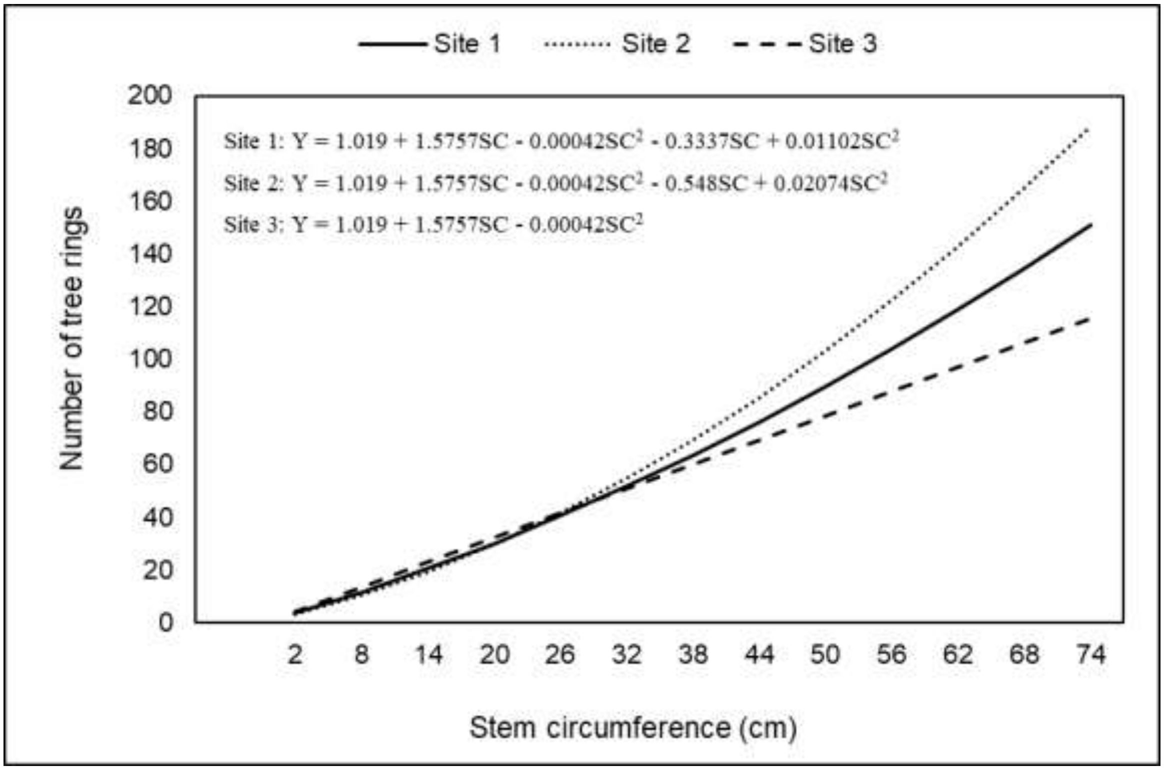

**Figure 6.1** Relationships between the number of growth rings and stem circumference of Vachellia tortilis at the three sites.

**Table 6.3** Correlation matrix for correlations between the number of growth rings and different growth parameters of *Vachellia tortilis.*

| | Growth rings | Stem circumference | Tree height | Crown diameter |
|---|---|---|---|---|
| Growth rings | - | 0.98** | 0.85** | 0.69** |
| Stem circumference | 0.98** | - | 0.66** | 0.87** |
| Tree height | 0.85** | 0.66** | - | 0.63** |
| Canopy diameter | 0.69** | 0.87** | 0.6240** | - |

*** = Highly significant at P < 0.01*

**Table 6.4** Pearson's coefficients of correlation for differences between relationships (number of growth rings and stem circumference of *Vachellia tortillis*) at the different sites

| Parameter | Estimate | Standard Error. | T (n=142) | t pr. |
|---|---|---|---|---|
| Constant | 1.02 | 0.92 | 1.11 | NS |
| SC Linear | 1.58 | 0.08 | 18.60 | ** |
| SC Quadratic | -0.00042 | 0.00132 | -0.32 | NS |
| SC Linear Site 1 | -0.33 | 0.08 | -4.01 | ** (1) |
| SC Linear Site 2 | -0.55 | 0.10 | -5.38 | ** (1) |
| SC Linear Site 3 | 0 | * | * | * (1) |
| SC Quadratic Site 1 | 0.01 | 0.00167 | 6.59 | ** (1) |
| SC Quadratic Site 2 | 0.02074 | 0.00259 | 8.02 | ** (1) |
| SC Quadratic Site 3 | 0 | * | * | * |

*** = Highly significant at P <.001*

** = Significant at P <.005*

*NS = Not significant*

**Table 6.5** Correlation between tree age and tree height within height classes

| **Height class** | **Tree height vs. Tree age** |
|---|---|
| >0.0 – 0.5 | .0267 |
| >0.5 – 1.5 | .1009 |
| >1.5 – 2.0 | .3752 |
| >2.0 – 3.0 | .3575 |
| >3.0 | .2537 |

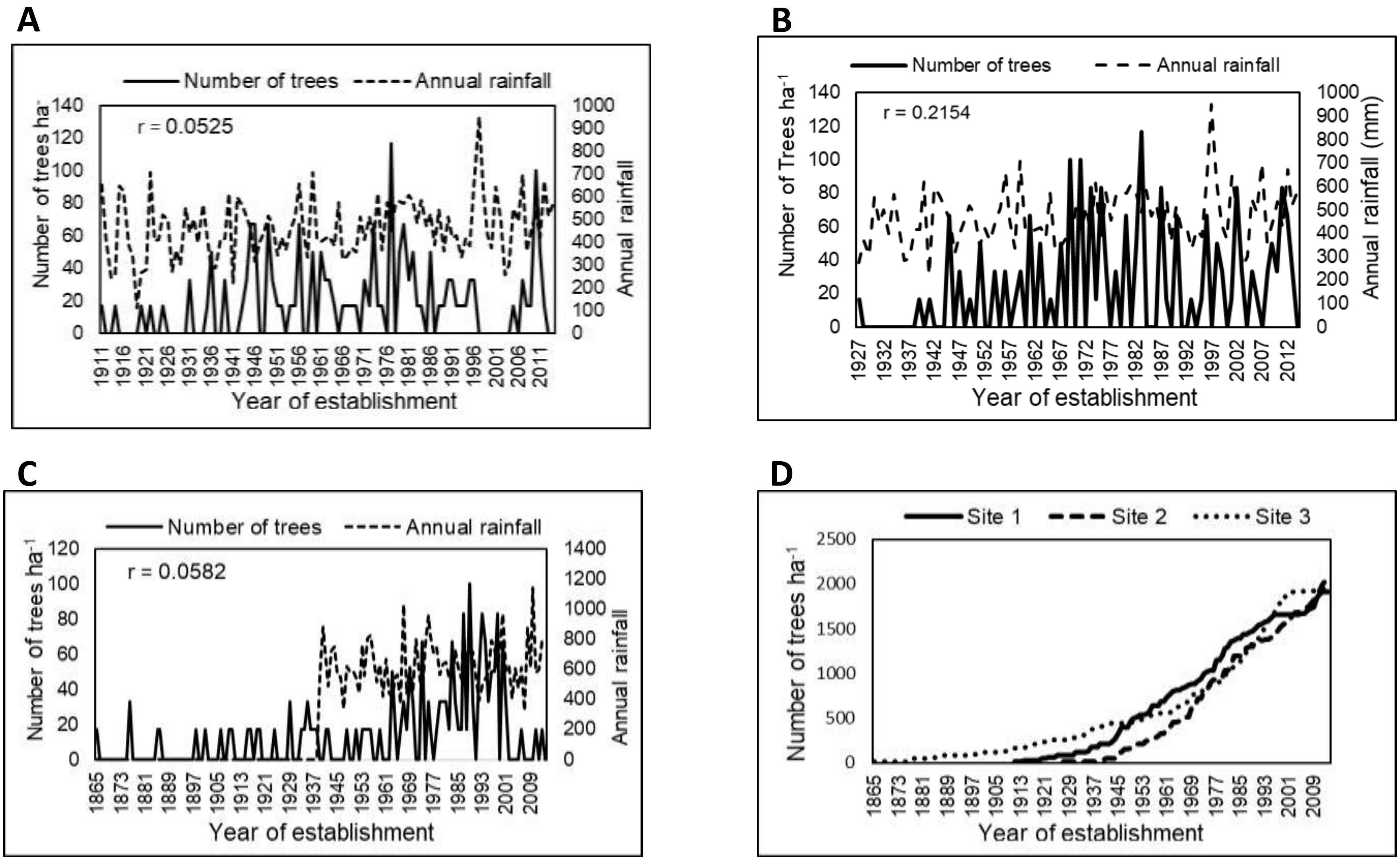

**Figure 6.2** The establishment patterns of *Vachellia tortilis* at Site 1 (A), Site 2 (B), and Site 3 (C), and the cumulative establishment of *Vachellia tortilis* at the three sites (D)

# CHAPTER 7: GENERAL CONCLUSIONS

## 7.1 INTRODUCTION

This thesis examined the effects of drought and grazing on dryland grasslands in the Limpopo Province of South Africa. This study's overarching objective was to generate data that will provide a better understanding of the dynamics of vegetation and insight into management strategies for rangelands in the face of climate and land-use change. The following are some of the motivations behind the conception of this study: (i) a significant portion of South Africa's dryland rangelands are grossly undermanaged, resulting in the severe degeneration of the savanna ecosystem; (ii) climate change is expected to increase the frequency of extreme climatic events such as droughts, floods, and heat waves; and (iii) communal areas are multi-use landscapes that are transformed by a number of interacting factors. The combination of these elements constitutes a threat to the livelihood of millions of people in South Africa because this ecosystem is accountable for a wide variety of services.

As the population of South Africa and the globe as a whole grows, there is a growing urgency to preserve or expand the functions and services provided by ecosystems and to improve food security, despite the fact that both the quantity and the quality of available land resources are decreasing. An additional reason for carrying out this research was the paucity of information available regarding the influence of drought and grazing on the ecological processes that occur in dryland grasslands (Chapter 1). In addition, a literature assessment was undertaken on the effects of climate change on the ecosystem services and function of savannas, as well as the implications of these changes for the livelihoods of people whose lives depend on the health of these ecosystems. This assessment revealed that there is a scarcity of research on the effects of drought and grazing on dryland grasslands, resulting in a restricted management capacity (Chapter 2). As a result, the purpose of the study was to investigate and provide answers to the following research questions:

**Research question 1:** Which diversity-mediated factors have the greatest influence on ecosystem functions and services?

**Research question 2:** What is the relative importance of bottom-up mechanisms (such as competitive release following drought) and top-down mechanisms (grazing and drought) for the recruitment of an encroacher tree species?

**Research question 3:** What are the direct and indirect effects of changing climate and land-use on multiple ecosystem services delivered by Limpopo's savanna vegetation?

The general conclusion section is structured as follows so that concluding statements can be made on the research questions explored in depth earlier in the thesis, as well as on the problem statement connected to those questions:

The primary findings of the study are examined in the context of their corresponding research questions as the first step of the synthesis process. The implications of the findings to scientific knowledge, management, and policy are presented next. The final section includes a discussion of the study's recommendations and possible future research areas.

## 7.2 KEY FINDINGS AND IMPLICATIONS

To present answers to the research questions posed at the beginning of the study, each objective was subdivided into a different chapter in the thesis, and all key findings are presented in relation to the chapters in which they were discovered:

### 7.2.1 What characterizes winner & loser species? Effects of long-term drought & grazing (Chapter 4)

**Related objective(s):** Evaluate ecosystem functioning through the assessment of climate-related taxonomic diversity and density demography from the grass layer (Objective 1), as well as the first part of the second objective: Analyse the effects of drought and grazing on the grass layer and to determine the factors affecting tree populations, particularly tree establishment patterns (objective 2).

**Hypothesis:** Ecosystem functioning is not determined, to a large extent, by taxonomic diversity and density demography from the grass layer.

**Which diversity-mediated factors have the greatest influence on ecosystem functions and services?**

To answer the aforementioned question, the DroughtAct experiment was implemented, a large-scale drought and grazing experiment that analyzes ecosystem performance under drought and non-drought conditions in grazed and un-grazed vegetation. The experiment was conducted in South African dryland grasslands. In this chapter, the effects of drought and grazing on all herbaceous vegetation were assessed to determine which species and plant functional types were resistant to the long-term effects of drought and grazing. In addition, the study was interested in the effect of grazing exclusion (resting) on species' ability to resist drought. The findings of the study demonstrated that most species and plant functional types lose to long-term drought and grazing. These findings allowed the hypothesis that "*ecosystem functioning is not determined, to a large extent, by taxonomic diversity and density demography from the grass layer*" to be rejected.

Isbell et al. (2015) discovered that grassland plant communities with a high diversity were not only more resistant to the effects of drought (they changed less), but they were also more robust (they recovered from drought more quickly) than communities with lower diversity. In addition, the research showed that the key functional traits that differentiate winners and losers were linked to disturbance tolerance, optimal resource acquisition, and low resource requirement. This provides the answer to the question *"What characteristics define winner and loser species and PFTs?".* The ability to distinguish between functional traits of winners and those of losers allows us to use the discovered characteristics as early indicators of veld degradation, so enabling timely management interventions.

### 7.2.2 Correlations between growth parameters and establishment of *Vachellia tortilis* (Forssk.) *Hayne* populations in the Limpopo Province, South Africa (Chapter 6)

**Related objective:** Analyse the effects of drought and grazing on the grass layer and determine the factors affecting tree populations, particularly tree establishment patterns (Objective 2). **Note:** this chapter answers the second part of this objective.

**Hypothesis:** Drought and grazing do not affect the grass layer and tree populations, particularly tree establishment patterns.

**What is the relative importance of bottom-up mechanisms (competitive release post-drought years) and top-down mechanisms (grazing and drought) for the recruitment of an encroacher tree species?**

The recruitment and establishment of encroacher tree species were investigated in this publication (Chapter 6), and the role that bottom-up mechanisms (different soil types) and top-down mechanisms (water limitation) play in the process were analyzed. To evaluate these mechanisms, research was carried out at two distinct geographic areas (three study sites total; two at location 2 and one at location 1), each of which had a distinct amount of rainfall (Sondela Nature Reserve and Syferkuil experimental farm at University of Limpopo). Two different soil types were examined. Because it was not possible to research all encroaching tree species in the province of Limpopo, *Vachellia tortilis* was chosen to represent encroaching tree species. In addition, this tree species was specifically chosen because it is one of the most invasive species in South Africa's dryland grasslands.

The facts reported in chapters 4 (winners and losers) and 6 (establishment of encroacher species) do not support the premise that "Drought and grazing do not affect the grass layer and tree populations, particularly tree establishment patterns." Therefore, this hypothesis is rejected. In chapter 4, the study revealed that drought and grazing had negative effects on herbaceous plants, whereas in chapter 6, it was shown that drought favoured the growth of *V. tortilis* (recruitment was greatest during years with the least precipitation). The results of the study showed that the type of soil had a greater influence on the establishment of *V. tortilis* than the amount of rainfall. This indicates that, in this context, bottom-up mechanisms had a greater impact on establishment than top-down mechanisms. However, the apparent lack of effect of precipitation on the development of invasive species can be attributable to the fact that the amount of precipitation at site 1 and location 2 differed very little. In order to determine the age of *V. tortilis*, the research involved the dating of woody trees and the assessment of the yearly growth increments, also known as tree rings. These tree rings were determined through destructive methods. After that, this information was plugged into a regression model alongside data on rainfall to have a better understanding of the relationship between rainfall and establishment. The discovery that there is a strong correlation between a tree's age and its stem circumference was therefore the most significant result of this study, suggesting that the age of a tree can be determined using a non-destructive technique.

### 7.2.3 Effect of drought and grazing on taxonomic and functional diversity (Chapter 5)

**Related objective(s):** Evaluate ecosystem functioning through the assessment of climate-related taxonomic diversity and density demography from the grass layer (Objective 1), as well as measure ecosystem service provision from the savanna ecosystem and also, to bridge the knowledge gap between local ecological knowledge and scientific research on the importance of biodiversity in an ecosystem (Objective 3).

Hypothesis: Propagation of the importance of ecosystem services from the savanna ecosystem to stakeholders will not bridge the knowledge gap between local ecological knowledge and scientific research for the proper management of the natural resource.

**What are the direct and indirect effects of changing climate and land-use on multiple ecosystem services delivered by Limpopo's savanna vegetation?**

In this chapter, one of the goals was to investigate the impact that drought, grazing, and resting have on the taxonomic and functional diversity of a community. The study examined diversity indices from grazed and ungrazed plants in both drought and non-drought conditions by using the DroughtAct experiment. The DroughtAct approach has several advantages, one of which is that it permits simultaneous modification and evaluation of multiple biotic and abiotic components of ecosystem function such as precipitation and grazing. The provision of ecosystem services by savanna rangelands under a variety of plausible future scenarios was assessed.

The results of the study showed that prolonged periods of drought and grazing have a direct negative impact on the taxonomic and functional diversity of the ecosystem. In general, drought treatments led to a reduction in taxonomic and functional richness and an increase in species evenness. Additionally, the species density per unit area was reduced. The decline in diversity that occurs as a direct result of drought has an indirect impact on the capacity of the ecosystem to offer services, for instance, Bellard et al. (2012) found that the ability of ecosystems to provide a service of climate management is dependent on the diversity of species that they currently support. In addition, the study shows that initially, resting has a favorable influence on diversity indices; but, as the length of the drought period increased, the impact of resting became negative, particularly for species richness.

### 7.2.4 Bridging the knowledge gap between scientific knowledge and local ecological knowledge (Chapter 2)

**Related objective(s):** Measure ecosystem service provision from the savanna ecosystem and also, bridge the knowledge gap between local ecological knowledge and scientific research on the importance of biodiversity in an ecosystem (Objective 3).

**Hypothesis:** There will be a gap between research and local ecological knowledge, leading to mismanagement of natural resources and, ultimately, a disproportionate loss in ecosystem services provided by savanna vegetation.

**What are the direct and indirect effects of changing climate and land-use on multiple ecosystem services delivered by Limpopo's savanna vegetation?**

The aim of this investigation was to determine factors impeding information sharing between LEK and scientific research. To achieve this goal the study examined pertinent literature. The results of this investigation indicated that scientists and lay people have a different understanding of the ecosystem function and services. Moreover, it has been reported that misperceptions among development actors regarding management interventions, strategies and pastoral life are the main drivers of development programs failure. However, there is a general consensus that sustainability in modern land-use, natural resource management, and conservation efforts can be achieved through direct involvement of all parties, as well as recognition of the knowledge and values that they hold. Therefore, bridging the knowledge gap between science and LEK requires the integration of LEK into contemporary science, thus development organizations with the essential understanding of pastoral systems. The hypothesis that "*Propagation of the importance of ecosystem services from the savanna ecosystem to stakeholders will not bridge the knowledge gap between local ecological knowledge and scientific research for the proper management of the natural resource."* can be accepted. Literature review suggests that the absence of accurate information from LEK is not the sole impediment to the proper management of natural resources; both knowledge systems contain differences that must be reconciled.

### 7.3 RECOMMENDATIONS AND AREAS OF FUTURE RESEARCH

This study has shown that there are several gaps in the previously published research, some of which weren't able to be filled up by this particular investigation. These areas require greater research so that the understanding and comprehension of the dynamics of the vegetation in response to changes in climate may be expanded. From this thesis, the following are some recommendations and potential areas for further research:

- Pertinent literature review showed that there is a substantial need for research on drought, an extreme climatic state that will likely occur in the future. This is primarily owing to the fact that African drylands are especially vulnerable to the effects of climate change, but policymakers and conservationists working in dryland grasslands lack scientific data to guide their management strategies.
- The effect of climate change on the biodiversity and ecological services provided by dryland grasslands has not gotten nearly enough attention from researchers. Consequently, it is crucial to perform research on the connections between biodiversity, ecosystem services, and climate change in order to create effective management strategies for dryland grasslands that may be applied in response to future climate extremes.
- Future experiments involving drought and grazing should study the relationship between woody and herbaceous plant species, specifically the germination, establishment, recruitment, and survival of woody vegetation from grazed and un-grazed vegetation. This is a great opportunity to obtain a better understanding of the mechanisms and key drivers that contribute to the encroachment of bush in dryland grasslands.

- Collaboration with small-scale farmers that rely on communal rangeland for cattle grazing is recommended in the future, to conduct research that combines local ecological knowledge and scientific research.
- Researching the combined effects of fertilization, grazing, and drought is also recommended.

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# APPENDIX S1

**Table 7.1.** Table outlines two main factors in the DroughtAct experiment, [1]Drought & [2]Grazing, and their respective levels. Furthermore, all the possible treatment combinations are shown.

| **Factors** | |
|---|---|
| **Drought** | **Grazing** |
| Drought + (D+) | Grazing + (G+) |
| Drought - (D-) | Grazing - (G-) |
| **Treatments** | |
| Treatment 1 | D+ G+ |

| | |
|---|---|
| Treatment 2 | D+ G- |
| Treatment 3 | D- G+ |
| Treatment 4 | D- G- |

**Table 7.2.** Six years grazing plan at Syferkuil Experimental Farm, DroughtAct camp.

| **Year** | **Growing Season** | | | | | | | | **Dry Season** | | | | | | | | | | | | **Growing Season** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Jan | | Feb | | March | | April | | May | | June | | July | | Aug | | Sep | | Oct | | Nov | | Dec | |
| 2014 | 🟩 | 🟩 | 🟨 | 🟨 | 🟨 | 🟩 | 🟩 | 🟨 | 🟨 | 🟨 | 🟨 | 🟨 | 🟩 | 🟨 | 🟨 | 🟨 | 🟨 | 🟨 | 🟩 | 🟨 | 🟨 | 🟨 | 🟨 | 🟨 |
| 2015 | 🟩 | 🟩 | 🟨 | 🟨 | 🟨 | 🟩 | 🟩 | 🟨 | 🟨 | 🟨 | 🟨 | 🟨 | 🟩 | 🟨 | 🟨 | 🟨 | 🟨 | 🟨 | 🟩 | 🟨 | 🟨 | 🟨 | 🟨 | 🟨 |
| 2016 | 🟩 | 🟩 | 🟨 | 🟨 | 🟨 | 🟩 | 🟩 | 🟨 | 🟨 | 🟨 | 🟨 | 🟨 | 🟩 | 🟨 | 🟨 | 🟨 | 🟨 | 🟨 | 🟩 | 🟨 | 🟨 | 🟨 | 🟨 | 🟨 |
| 2017 | 🟨 | 🟩 | 🟩 | 🟨 | 🟨 | 🟨 | 🟩 | 🟩 | 🟨 | 🟨 | 🟨 | 🟨 | 🟩 | 🟨 | 🟨 | 🟨 | 🟨 | 🟨 | 🟩 | 🟨 | 🟨 | 🟨 | 🟨 | 🟨 |
| 2018 | 🟨 | 🟩 | 🟩 | 🟨 | 🟨 | 🟨 | 🟩 | 🟩 | 🟨 | 🟨 | 🟨 | 🟨 | 🟩 | 🟨 | 🟨 | 🟨 | 🟨 | 🟨 | 🟩 | 🟨 | 🟨 | 🟨 | 🟨 | 🟨 |
| 2019 | 🟨 | 🟩 | 🟩 | 🟨 | 🟨 | 🟨 | 🟩 | 🟩 | 🟨 | 🟨 | 🟨 | 🟨 | 🟩 | 🟨 | 🟨 | 🟨 | 🟨 | 🟨 | 🟩 | 🟨 | 🟨 | 🟨 | 🟨 | 🟨 |
| 2020 | 🟨 | 🟩 | 🟩 | 🟨 | 🟨 | 🟨 | 🟩 | 🟩 | 🟨 | 🟨 | 🟨 | 🟨 | 🟩 | 🟨 | 🟨 | 🟨 | 🟨 | 🟨 | 🟩 | 🟨 | 🟨 | 🟨 | 🟨 | 🟨 |

**Key**

🟩 Grazing by 25 – 30 herd of cattle

🟨 Resting

**Table 7.3.** An outline of all grasses species that were identified at the DroughtAct experiment throughout the study period (2014 to 2020), described by their life cycle and plant functional type.

| **DROUGHTACT GRASS SPECIES LIST** | | |
|---|---|---|
| Grass species | Plant Functional Type | Description |
| 1. Aristida aequiglumis Hack. | Narrow-leaved | Perennial |
| 2. Aristida congesta | Broad-leaved | Perennial |
| 3. Aristida diffusa | Narrow-leaved | Perennial |
| 4. Aristida stipitata Hack. | Narrow-leaved | Perennial |
| 5. Brachiaria nigropedata | Broad-leaved | Perennial |

|  |  |  |
|---|---|---|
| 6. Chloris virgata | Annual | Annual |
| 7. Dactyloctenium aegyptium | Annual | Annual |
| 8. Dactyloctenium giganteum | Annual | Annual |
| 9. Digitaria eriantha | Very Broad-leaved | Perennial |
| 10. Elionurus muticus | Narrow-leaved | Perennial |
| 11. Eragrostis lehmanniana | Narrow-leaved | Perennial |
| 12. Eragrostis rigidior | Narrow-leaved | Perennial |
| 13. Eragrostis superba | Broad-leaved | Perennial |
| 14. Heteropogon contortus | Broad-leaved | Perennial |
| 15. Melinis repens | Annual | Annual |
| 16. Microchloa caffra | Narrow-leaved | Perennial |
| 17. Panicum maximum | Very Broad-leaved | Perennial |
| 18. Pogonarthria squarrosa | Broad-leaved | Perennial |
| 19. Schmidtia pappophoroides | Broad-leaved | Perennial |
| 20. Sporobolus festivus | Narrow-leaved | Perennial |
| 21. Sporobolus ioclados | Broad-leaved | Perennial |
| 22. Stipagrostis uniplumis | Broad-leaved | Perennial |
| 23. Themeda triandra | Broad-leaved | Perennial |
| 24. Tragus berteronianus | Annual | Annual |
| 25. Trichoneura grandiglumis | Broad-leaved | Perennial |
| 26. Tricholaena monachne | Broad-leaved | Perennial |
| 27. Urochloa mosambicensis | Broad-leaved | Perennial |

# Appendix S2

### WINNERS AND LOSERS STATISTICAL ANALYSIS

Generalized Linear Model (GLM)

(i) Model1: PFT ~ Drought*Grazing

(ii) Model2: PFT ~ Drought*Grazing*SampYear

**Effect of long-term drought and grazing on PFTs**

**Table 7.4.** Effect of drought and grazing on the biomass production of forbs over the study period

| Effect of long-term drought and grazing on Forbs | | | |
|---|---|---|---|
| | **Drought** (p-value) | **Grazing** (p-value) | **Drought*Grazing** (p-value) |
| 2015 | 0.508 | 0.203 | 0.546 |
| 2016 | 0.120 | 0.120 | 0.465 |
| 2017 | 0.670 | 0.085 | 0.755 |
| 2018 | 0.879 | 0.980 | 0.997 |
| 2019 | 0.071 | 0.509 | 0.524 |
| 2020 | 0.416 | 0.120 | 0.157 |

**Table 7.5.** Effect of drought and grazing on the biomass production of narrow-leaved grass over the study period

| Effect of long-term drought and grazing on Narrow-leaved grasses | | | |
|---|---|---|---|
| | **Drought** | **Grazing** | **Drought*Grazing** |
| 2015 | 0.952 | 0.218 | 0.407 |
| 2016 | 0.918 | 0.608 | 0.621 |
| 2017 | 0.995 | 0.0001 ** | 0.125 |
| 2018 | 0.987 | 0.623 | 0.742 |
| 2019 | 0.741 | 0.263 | 0.334 |
| 2020 | 0.47987 | 0.001 ** | 0.001 ** |

**Table 7.6.** Post hoc test of significant relationships – Narrow-leaved grass 2017

| NARROW-LEAVED GRASSES: YEAR 3 (2017) | | | | | |
|---|---|---|---|---|---|
| **Treatment mean** | | | | **Treatment comparison** | |
| Drought | Grazing | Emmean | SE | Drought:Grazing | P-value |
| y | y | 1.59 | 0.295 | y:n-n:n | 0.9999997 |
| n | y | 2.38 | 0.182 | n:y-n:n | 0.0026348 ** |
| y | n | 3.57 | 0.295 | y:y-n:n | 0.0038587 ** |
| n | n | 3.57 | 0.223 | n:y-y:n | 0.0164101 * |
| | | | | y:y-y:n | 0.0126352 * |

| | |
|---|---|
| y:y-n:y | 0.8767413 |

**Table 7.7.** Post hoc test of significant relationships – Narrow-leaved grass 2020

| **NARROW-LEAVED GRASSES: YEAR 6 (2020)** | | | | | |
|---|---|---|---|---|---|
| **Treatment mean** | | | | **Treatment comparison** | |
| Drought | Grazing | Emmean | SE | Drought:Grazing | P-value |
| n | n | 1.355 | 0.308 | y:n-n:n | 0.9793571 |
| y | n | 1.726 | 0.420 | n:y-n:n | 0.0126599 * |
| n | y | 2.648 | 0.222 | y:y-n:n | 0.9842900 |
| y | y | 0.969 | 0.269 | n:y-y:n | 0.1636177 |
| | | | | y:y-y:n | 0.8959118 |
| | | | | y:y-n:y | 0.0015666 ** |

**Table 7.8.** Effect of drought and grazing on the biomass production of broad-leaved grass over the study period

| **Effect of long-term drought and grazing on broad-leaved grasses** | | | |
|---|---|---|---|
| | **Drought** | **Grazing** | **Drought*Grazing** |
| 2015 | 0.757 | 0.877 | 0.713 |
| 2016 | **0.0348 *** | 0.4797 | 0.3809 |
| 2017 | 0.4909 | **0.0065 **** | 0.4732 |
| 2018 | 0.0876 | **0.0299 *** | 0.7731 |
| 2019 | 0.2667 | **0.0008 ***** | 0.0933 |
| 2020 | **0.0111 *** | **0.0470 *** | 0.8443 |

**Table 7.9.** Post hoc test of significant relationships – Broad-leaved grass 2016

| BROAD-LEAVED GRASSES: YEAR 2 (2016) | | | | | |
|---|---|---|---|---|---|
| **Treatment mean** | | | | **Treatment comparison** | |
| Drought | Grazing | Emmean | SE | Drought:Grazing | P-value |
| n | n | 3.21 | 0.233 | n:n – y:n | 0.1441 |
| y | n | 2.49 | 0.247 | n:n – n:y | 0.8938 |
| n | y | 3.41 | 0.162 | n:n – y:y | 0.9396 |
| y | y | 3.05 | 0.160 | y:n – n:y | 0.0095 ** |
| | | | | y:n – y:y | 0.2272 |
| | | | | n:y – y:y | 0.3808 |

**Table 7.10.** Post hoc test of significant relationships – Broad-leaved grass 2017

| BROAD-LEAVED GRASSES: YEAR 3 (2017) | | | | | |
|---|---|---|---|---|---|
| **Treatment mean** | | | | **Treatment comparison** | |
| Drought | Grazing | Emmean | SE | Drought:Grazing | P-value |
| y | y | 2.53 | 0.192 | y:n-n:n | 0.6276920 |
| n | y | 3.14 | 0.159 | n:y-n:n | 0.0018337 ** |
| y | n | 3.72 | 0.295 | y:y-n:n | 0.0000435 *** |
| n | n | 3.99 | 0.264 | n:y-y:n | 0.2010737 |
| | | | | y:y-y:n | 0.0177128 * |
| | | | | y:y-n:y | 0.4102927 |

**Table 7.11.** Post hoc test of significant relationships – Broad-leaved grass 2018

| BROAD-LEAVED GRASSES: YEAR 4 (2018) | | | | | |
|---|---|---|---|---|---|
| **Treatment mean** | | | | **Treatment comparison** | |
| Drought | Grazing | Emmean | SE | Drought:Grazing | P-value |
| y | n | 1.50 | 0.392 | n:n - y:n | 0.3082 |
| y | y | 2.28 | 0.259 | n:n - n:y | 0.1200 |
| n | n | 2.28 | 0.226 | n:n - y:y | 1.0000 |
| n | y | 2.90 | 0.166 | y:n - n:y | 0.0054 ** |
| | | | | y:n - y:y | 0.3461 |

| | |
|---|---|
| n:y - y:y | 0.1776 |

**Table 7.12.** Post hoc test of significant relationships – Broad-leaved grass 2019

| **BROAD-LEAVED GRASSES: YEAR 5 (2019)** | | | | | |
|---|---|---|---|---|---|
| **Treatment mean** | | | | **Treatment comparison** | |
| Drought | Grazing | Emmean | SE | Drought:Grazing | P-value |
| y | y | 1.27 | 0.293 | y:n-n:n | 0.2812452 |
| n | y | 2.69 | 0.166 | n:y-n:n | 0.0002176 *** |
| y | n | 3.26 | 0.349 | y:y-n:n | 0.0000385 *** |
| n | n | 3.74 | 0.258 | n:y-y:n | 0.4981744 |
| | | | | y:y-y:n | 0.0903015 |
| | | | | y:y-n:y | 0.3901722 |

**Table 7.13.** Post hoc test of significant relationships – Broad-leaved grass 2020

| **BROAD-LEAVED GRASSES: YEAR 6 (2020)** | | | | | |
|---|---|---|---|---|---|
| **Treatment mean** | | | | **Treatment comparison** | |
| Drought | Grazing | Emmean | SE | Drought:Grazing | P-value |
| y | y | 1.16 | 0.291 | y:n-n:n | 0.0354403 * |
| y | n | 1.85 | 0.487 | n:y-n:n | 0.0245361 * |
| n | y | 2.59 | 0.192 | y:y-n:n | 0.0005424 *** |
| n | n | 3.41 | 0.363 | n:y-y:n | 0.7931946 |

| | |
|---|---|
| y:y-y:n | 0.9805536 |
| y:y-n:y | 0.1906352 |

**Table 7.14.** Effect of drought and grazing on the biomass production of broad-leaved grass over the study period

| **Effect of long-term drought and grazing on very broad-leaved grasses** | | | |
|---|---|---|---|
| | **Drought** | **Grazing** | **Drought*Grazing** |
| 2015 | 0.306 | 0.329 | 0.876 |
| 2016 | 0.259 | **0.022** * | 0.947 |
| 2017 | **0.004** ** | 0.227 | 0.888 |
| 2018 | **0.0015** ** | 0.8059 | NA |
| 2019 | 0.548 | 0.887 | 0.459 |
| 2020 | 0.095 | 0.687 | 0.419 |

**Table 7.15.** Post hoc test of significant relationships – Very-broad-leaved grass 2016

| **VERY BROAD-LEAVED GRASSES: YEAR 2 (2016)** | | | | | |
|---|---|---|---|---|---|
| **Treatment mean** | | | | **Treatment comparison** | |
| Drought | Grazing | Emmean | SE | Drought:Grazing | P-value |
| y | n | 2.08 | 0.510 | n:n - y:n | 0.6581 |
| n | n | 2.76 | 0.295 | n:n - n:y | 0.0755 |
| y | y | 3.08 | 0.279 | n:n - y:y | 0.8536 |
| n | y | 3.71 | 0.266 | y:n - n:y | 0.0234 * |
| | | | | y:n - y:y | 0.3106 |
| | | | | n:y - y:y | 0.3592 |

**Table 7.16.** Post hoc test of significant relationships – Very-broad-leaved grass 2017

| **VERY BROAD-LEAVED GRASSES: YEAR 3 (2017)** | | | | | |
|---|---|---|---|---|---|
| **Treatment mean** | | | | **Treatment comparison** | |
| Drought | Grazing | Emmean | SE | Drought:Grazing | P-value |
| y | y | 2.35 | 0.218 | n:n - y:n | 0.0116 * |
| y | n | 2.63 | 0.487 | n:n - n:y | 0.6053 |
| n | y | 3.88 | 0.218 | n:n - y:y | <.0001 *** |
| n | n | 4.26 | 0.208 | y:n - n:y | 0.0872 |
| | | | | y:n - y:y | 0.9510 |
| | | | | n:y - y:y | <.0001 *** |

**Table 7.17.** Post hoc test of significant relationships – Very-broad-leaved grass 2018

| **VERY BROAD-LEAVED GRASSES: YEAR 4 (2018)** | | | | | |
|---|---|---|---|---|---|
| **Treatment mean** | | | | **Treatment comparison** | |
| Drought | Grazing | Emmean | SE | Drought:Grazing | P-value |
| n | n | 2.922 | 0.350 | n:n - y:n | NA |
| y | n | nonEst | NA | n:n - n:y | 0.9945 |
| n | y | 3.035 | 0.286 | n:n - y:y | 0.0030 ** |
| y | y | 0.823 | 0.495 | y:n - n:y | NA |
| | | | | y:n - y:y | NA |
| | | | | n:y - y:y | 0.0006 *** |

**Table 7.18.** Drought vs. Non-drought: Effect of resting on narrow-leaved grasses over the study period

| | Effect of long-term drought and grazing on Narrow-leaved grasses | |
|---|---|---|
| | D-G- vs. D-G+ (P-value) | D+G- vs. D+G+ (P-value) |
| 2015 | 0.7488135 | 0.9999978 |
| 2016 | 0.9757161 | 0.6358593 |
| 2017 | 0.0026348 ** | 0.0126352 * |
| 2018 | 0.9620869 | 0.9999982 |
| 2019 | 0.2608169 | 0.3906214 |
| 2020 | 0.0126599 * | 0.8959118 |

**Table 7.19.** Drought vs. Non-drought: Effect of resting on broad-leaved grasses over the study period

| | Example: effect of long-term drought and grazing on Broad-leaved grasses | |
|---|---|---|
| | D-G- vs. D-G+ | D+G- vs. D+G+ |
| 2015 | 0.9984221 | 0.9073142 |
| 2016 | 0.8655956 | 0.6129622 |
| 2017 | 0.0018337 ** | 0.0177128 * |
| 2018 | 0.1515677 | 0.8549194 |
| 2019 | 0.0002176 *** | 0.0903015 * |
| 2020 | 0.0245361 * | 0.9805536 |

**Table 7.20.** Drought vs. Non-drought: Effect of resting on very-broad-leaved grass over the study period

| | Example: effect of long-term drought and grazing on Very Broad-leaved grasses | |
|---|---|---|
| | D-G- vs. D-G+ (P-value) | D+G- vs. D+G+ (P-value) |
| 2015 | 0.7065441 | 0.8542425 |
| 2016 | 0.1971561 | 0.8707721 |
| 2017 | 0.4423765 | 0.9991153 |
| 2018 | 0.1515677 | 0.8549194 |
| 2019 | 0.9987618 | 0.9967565 |
| 2020 | 0.9828420 | 0.9999380 |

**Table 7.21.** Proportion of PFTs biomass production per treatment

| PFT | D-G+ | D-G- | D+G- | D+G+ |
|---|---|---|---|---|
| **Annual** | 0.0380 | 0.0528 | 0.0315 | 0.0323 |
| **Broad-leaved** | 0.608 | 0.598 | 0.537 | 0.502 |
| **Very Broad-leaved** | 0.1388 | 0.1855 | 0.0356 | 0.0730 |
| **Forb** | 0.0920 | 0.0762 | 0.1650 | 0.2279 |
| **Narrow-leaved** | 0.138 | 0.137 | 0.224 | 0.146 |