GRASS SPECIES RECOVERY FROM COMBINED EFFECTS OF LONG-TERM DROUGHT AND GRAZING, UNDER NITROGEN FERTILIZATION IN SEMI-ARID SAVANNA ECOSYSTEM, IN LIMPOPO PROVINCE, SOUTH AFRICA

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MASETE MARTIN LEBEYA

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SUPERVISOR: PROF KK AYISI

CO-SUPERVISOR: DR LM MOTSHEKGA

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DECLARATION

I <u>Lebeya Masete Martin</u>, declare that the mini-dissertation hereby submitted to the University of Limpopo, for the degree Master of Science in Pasture Science has not previously been submitted by me for a degree at this or any other university; that it is my work in design and in execution, and that all materials contained herein has been duly acknowledged

Lebeya MM

14 February 2024

Surnames, Initials

Date

DEDICATION

I am dedicating my work to my late parents Albert Lebeya, Phuti Elina Monno and my aunt Olitha Lehong.

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Philippians Chapter 4 verse 13 (KJV) "I can do all things through Christ who strengthens me."

I would like to give thanks to God for His strength and unconditional love

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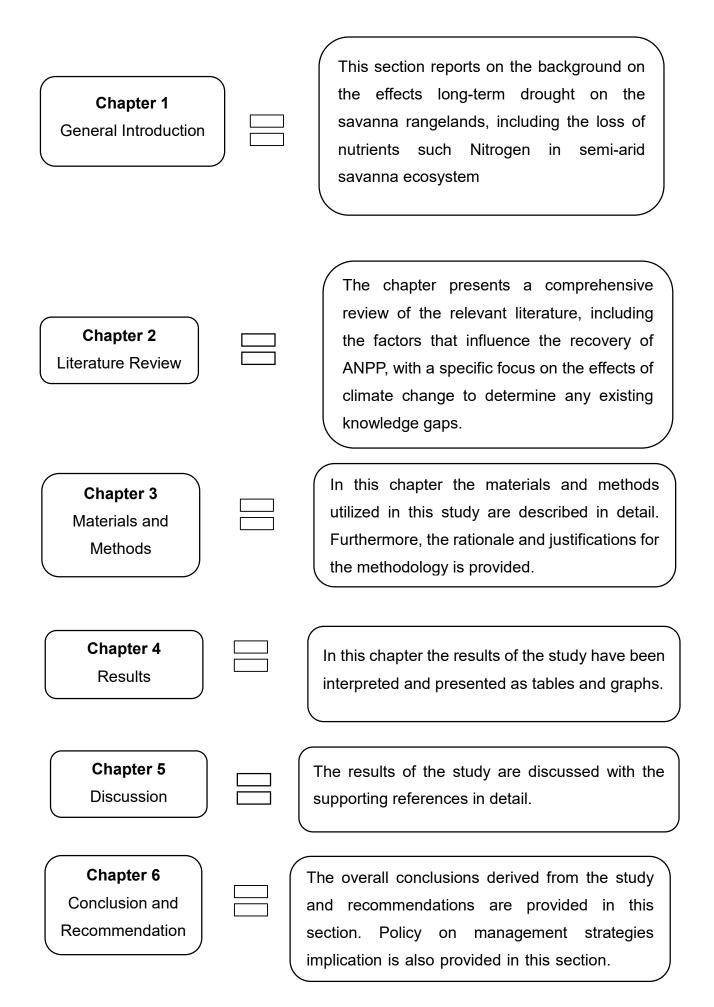
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LIST OF ACRONYMS AND MEANING

| ANPP | = Aboveground net primary production |
|-------------|--------------------------------------|
| AGB | = Aboveground biomass |
| Aris.cong | = Aristida congesta |
| Aris.diff | = Aristida diffusa |
| Aris.stip | = Aristida stipitata |
| Brac.nigr | = Bracharia nigropedata |
| Bulb.hisp | = Bulbostlylis hispidula |
| Chlo.viga | = Chloris virgata |
| Dact.aegy | = Dactyloctenium aegyptium |
| Digi.eria | = Digitaria eriantha |
| (D+) | = Drought |
| Dico.tome | = Dicoma tomentosa |
| (D-) | = Non drought |
| Erag.lehm | = Eragrostis lehmanniana |
| Erag.rigi | = Eragrostis rigidior |
| Erag.supe | = Eragrostis superba |
| GRA | = Grazed plots |
| (G+) | = Grazing |
| (G-) | = No grazing |
| HG ova = Ve | ery-broad-leaved |
| HG lan | = Broad-leaved |
| HG lin | = Narrow-leaved |
| Hete.cont | = Heteropogon conturtus |

| Kg | = Kilo gram |
|--------------------|--------------------------------|
| Kyll.alba | = Kyllinga alba |
| LSU | = Livestock unit |
| LAN | = Limestone Ammonium Nitrate |
| LTEs | = Long-term grazing exclosures |
| Meli.repe | = Melenis repens |
| Micr.caff | = Microchloa caffra |
| Ν | = Nitrogen |
| N ha ⁻¹ | = Nitrogen per hectare |
| PFTs | = Plant functional type |
| Pogo.squam | = Pogonarthria saquarrosa |
| Pani.maxi | = Panicum maximum |
| Pogo.saqua | = Pogonarthria saquarrosa |
| STEs | = Short-term exclosure |
| Schm.papp | = Schmidtia pappophoroides |
| Them.tria | = Themeda triantra |
| Tric.mon | = Tricholaena monachne |
| Trig.gran | = Trichoneura. grandiglumis |
| Uroc.mosa | = Urochloa mosambicencis |
| | |

MINI DISSERTATION STRUCTURE



ABSTRACT

Savanna ecosystems are naturally occurring ecosystems in arid or semi-arid regions that are well-suited for commercial and communal farming practices, particularly for grazing livestock. Climate change-induced drought is currently threatening this precious resource and increasing nitrogen (N) loss because of increased asynchrony between N mineralization and uptake by plants. A "DroughtAct" experiment was initiated to investigate the effects of nitrogen on ecosystem functions and services from grazed (G+) and ungrazed (G-) vegetation, under drought (D+) and non-drought (D-) conditions. The experiment consisted of four blocks that combined drought treatments with grazing treatments, which were replicated six times, resulting in 24 plots (10 x 10 m each) separated by 5 m wide corridors. For the purpose of this study, the rain-out shelter treatments were removed after six years to study vegetation recovery through evaluation of aboveground net primary production (ANPP). The data collected in the last year of drought was compared with the first two years of recovery (2021 and 2022). From the findings, no significant ANPP difference (P≤0.05) was found between the last year of drought and the first two years of recovery. However, a high ANPP was recorded under post-drought treatment at 13.93g/m² compared to drought treatment at 2.24 g/m² in 2022. Furthermore, a significant (P≤0.05) ANPP recovery was recorded under grazed treatment in the second year of recovery. Furthermore, the application of nitrogen fertilization exhibited negligible impact (P≥0.0.5) on the drought treatments' aboveground net primary productivity (ANPP) range. The biomass production exhibited no significant variation across the different treatments, generally falling within the range of 31.73 to 32.12 (g/m²). The study showed that the combined effect of drought and grazing has a negative effect on ANPP recovery. The study highlights the resilience of savanna ecosystems in recovering from drought-induced stress on ANPP, while also emphasizing the importance of considering grazing management and water stress adaptation when studying ecosystem functions and services in the context of climate change.

Keywords: Aboveground net primary production, Drought, Recovery

CHAPTER 1: GENERAL INTRODUCTION

1.1 Background

Livestock farming is an important component of agriculture in South Africa and elsewhere, supplying food for both urban and rural populations, drought and overgrazing are key causes of grassland degradation by reducing vegetation cover and affecting plant nutrition (Yong-Zhong *et al.*, 2005; Hilker *et al.*, 2014; Hurley *et al.*, 2015). In South Africa, approximately 80% of agricultural land is suited for intensive grazing (Hendricks *et al.*, 2016). Each animal grazes across a broad area with little labor and expenditure in extensive grazing (Pulido *et al.*, 2018).

For productivity, cattle farmers in many rural communities frequently adopt this sort of grazing, in which cattle solely graze on natural rangeland (Nyamushamba *et al.*, 2017; Mapiye *et al.*, 2018). These communal grazing lands are overgrazed and therefore cannot provide adequate nutrients for a good level of productivity among livestock (Matlebyane *et al.*, 2010). Degradation of rangelands reduces vegetation cover, palatable grass species and soil quality leading to depletion of soil nutrients (Kassahun *et al.*, 2008).

Savanna ecosystems occupy 46% of semi-arid to arid regions of South Africa (Fox *et al.*, 2017). It is defined as a periodic ecosystem denoted by the co-dominance of a herbaceous continuous layer, C4 grasses dominated, and an erratic layer of trees and fire-tolerant shrubs (Ratnam *et al.*, 2011). The co-dominance characteristic in savannas between trees and grasses provides essential ecosystem services (Conner *et al.*, 2005). In rural areas, savanna rangelands provide essential services mainly grazing (Thiaw, 2015; Ryan *et al.*, 2016). Many savanna rangelands are under heavy pressure due to intensification of land use, expansion of settlements, as well as climate change, particularly drought (Niang *et al.*, 2014).

Droughts, defined as periods of below-average rainfall and above-average temperature, have been increasing in frequency and intensity in southern Africa in recent decades, likely linked to global climate change (Dai, 2013; van Wilgen *et al.*, 2016; Tadross *et al.*, 2017; Maúre *et al.*, 2018; Nkemelang *et al.*, 2018). Under climate change, drought was and is still an acute problem that affects plant growth, and ecosystem productivity, in many regions all over the world, particularly in arid and

semi-arid areas (Leemans *et al.*, 2006). According to Knapp *et al.* (2015), rangelands semi-arid are the most susceptible to drought among grasslands with aboveground net primary production, drought-induced herbaceous cover loss causes a significant increase in soil erosion by both water and wind, as well as a loss of soil nutrients (Li *et al.*, 2013).

According to He and Dijkstra (2014), a recent meta-analysis demonstrated that drought stress decreases the concentration of nitrogen (N) in plant tissue, and several studies have shown that drought can decrease nutrient uptake from soil (Cramer *et al.*, 2009; Waraich *et al.*, 2011; Ge *et al.*, 2012; Sardans and Peñuelas, 2012). Decreased nutrient uptake during drought may occur for several reasons, including the reduction of nutrient supply through mineralization (Fierrer and Schimel, 2002; Schimel *et al.*, 2007; Sanaullah *et al.*, 2012).

Grasslands are a highly prevalent type of terrestrial ecosystem found across the globe, exhibiting a wide distribution and encompassing vast areas of land (Dixon *et al.*, 2014). In some cases, this situation creates pressure to expand grasslands to areas outside of native vegetation (Garret *et al.*, 2018). Intensification of grasslands in these areas is an option to reverse this situation (Oenema *et al.*, 2014). Strategies of grassland-use intensification are expected to increase further, especially in humid and sub-humid environments (Thornton, 2010), where soil humidity is not a limiting factor for most of the year (Pandey *et al.*, 2011). One means of intensifying livestock production in grasslands is by fertilizing pastures with nitrogen (N) and optimizing the proportion of forage consumed by animals through grazing management (Lemaire, 2012).

Nitrogen is an essential structural constituent of proteins, rubisco, nucleic acids, and chlorophyll in addition to some hormones, and its application in the form of fertilization is a vital agronomic management strategy to boost crop performance (Ata-UI-Karim *et al.,* 2016).

The majority of remaining native Savannas are either lacking proper protection or management and as a result, are being lost at an alarming rate. This underscores the importance of local grassland restoration to achieve sustainable livestock production in a changing climate (Nerlekar and Veldman, 2020). Therefore, the implementation of appropriate management practices is of paramount importance to ensure the

sustainability of the ecosystem and to maintain the ecological value of grasslands (Tilman *et al.*, 2001).

1.2 Problem Statement

Savanna ecosystems are naturally occurring in arid or semi-arid regions that are wellsuited for commercial and communal farming practices, particularly for grazing livestock (Zerga, 2015; Molefi and Mbajiorgu, 2017). The savanna ecosystem plays a critical role in providing the vast majority of forage required to sustain livestock populations (Aydin and Uzun, 2004). Drought is currently threatening this precious resource and increasing nitrogen (N) loss because of increased asynchrony between N mineralization and uptake by plants (Knapp *et al.*, 2001; Haddad *et al.*, 2002; Chaves *et al.*, 2003; Leemans *et al.*, 2006).

Nitrogen is a critical limiting resource, and alterations in its availability are expected to impact the outcome of competition between trees and grasses (van Der Waal *et al.*, 2009). However, due to savanna ecosystem degradation in South Africa, communal farmers in particular frequently overstock rangelands (Jordaan *et al.*, 2013) causing overgrazing, which is the excessive removal of leafy biomass that inhibits grass regrowth (Li *et al.*, 2013). Overgrazing decreases forage production, especially on small farms (Shoroma, 2014). The availability of productive savanna rangelands is a growing concern for sustainable livestock production in South Africa, particularly for smallholder farmers. Suitable management practices for the sustainability of the savanna ecosystem are therefore crucial to maintaining the value of grasslands (Tilman *et al.*, 2001). Assessing grass species recovery after long-term drought, grazing, and fertilization of grasses could be an important management strategy for livestock farmers.

1.3 Rationale

Savanna rangelands provide a dual purpose by facilitating livestock grazing activities, while also serving as a key source of feed for livestock (Zerga, 2015). These rangelands provide food and other animal products for rural populations, generating profit from the sale of these items in the process (Asner *et al.*, 2004). Drought, which poses a threat to the functioning of savanna ecosystems and human livelihoods, is

anticipated to become more frequent, intense, and protracted because of climate change (van Wilgen *et al.*, 2016; Sankaran, 2019). In the past, savanna ecosystem rangelands have demonstrated resilience in the face of natural disasters such as drought (Vetter, 2009). Due to grasses' C4 pathways, they are drought tolerant (Ward *et al.*, 1999), while forbs might withstand drought through their deep root system (Nippert and Knapp, 2007). However, continuous grazing, in conjunction with climate change and variability, has increased savanna ecosystem rangeland's vulnerability to drought by reducing infiltration of soil water, reducing the grass layer, decreasing pasture production, increasing surface runoff, and changing savanna ecosystem rangeland species composition (Reece *et al.*, 2008).

Drought degrades the grass layer significantly, and the effects can last for up to a year (Staver et al., 2019). It may take decades for it to regain the grass layer's productive capacity, or the grass layer may recover rapidly with appropriate management interventions (Swemmer et al., 2018). Currently, grass species recovery after longterm drought and grazing in communal grazing savanna ecosystem rangelands of smallholder livestock producers is the subject of limited research, which contributes to the mismanagement of savanna ecosystem rangelands. Appropriate and sufficient fertilization of rangelands in the savanna ecosystem of Limpopo Province is reported as a viable and effective approach to increasing dry matter output on savanna ecosystem rangelands (Frame, 1992). Savanna ecosystem rangeland fertilization, particularly with N and phosphorus (P), can promote grass growth and boost dry matter production by two to three times, based on moisture and the yearly rainfall in the location (Lee and Lee, 2000; Elliott and Abbott, 2003). Understanding the recovery of savanna ecosystem grass from the impacts of combined long-term extreme drought, grazing and fertilization is critical for semi-arid rangeland management and conservation.

1.4 Aim

The aim of this scientific investigation was to generate empirical evidence that can advance the current understanding of the rehabilitation of herbaceous species under the compounded influence of prolonged drought, grazing, and nitrogen fertilizer application.

1.5 Objectives

The objectives of the study were to:

- Determine the recovery of grass species in a semi-arid savanna ecosystem after long-term drought and moderate grazing, through the evaluation of aboveground net primary production (ANPP) and standing biomass yield.
- Investigate the impact of a minimal dose of nitrogen fertilization on the grass species and biomass production after combined long-term drought and moderate grazing in a semi-arid savanna ecosystem.

1.6 Hypotheses

- The combination of long-term drought and moderate grazing in a semi-arid savanna ecosystem will not affect Aboveground Net Primary Production (ANPP) and standing biomass yield of grass species.
- The application of a minimal dose of nitrogen fertilizer to a semi-arid savanna ecosystem experiencing long-term drought and moderate grazing will not affect the biomass production of grass species in a semi-arid savanna ecosystem.

CHAPTER 2: LITERATURE REVIEW

2.1 Introduction

Trees and grasses predominate in savanna grasslands (Wiegan *et al.*, 2006). Savanna grasslands are under severe threat from ongoing degradation, undermining their capacity to support biodiversity, ecosystem services and human well- being (Bardgett *al.*, 2021). The main drivers of rangeland degradation comprise anthropogenic and natural factors (Mussa *et al.*, 2016). Natural variables responsible for rangeland degradation include climate change, aridity and desertification, drought, and bush encroachment, among others (Abate *et al.*, 2012; Mussa *et al.*, 2016). Amongst the anthropogenic factors, overstocking /overgrazing, population pressure, government policies, decline in traditional resource management institutions as well as changes in land use systems have been associated with rangeland degradation (Mussa *et al.*, 2016).

2.2 The savanna biome

A savanna biome is defined as a periodic ecosystem denoted by the co-dominance of herbaceous continuous layer, C4 grasses dominated, and an erratic layer of trees and fire tolerant shrubs (Ratnam *et al.*, 2011). Nine main biomes are found in South Africa, and their distribution is determined principally by temperature and the amount and seasonality of rainfall (Kayleigh *et al.*, 2016. Climate and other regulating factors likely affect grasses and trees differently, resulting in spatiotemporal heterogeneity of tree and grass compositions (Andric *et al.*, 2020). Savanna rangelands provide people with important ecosystem services, mainly livestock production and supply of fuelwood (Scheiter *et al.*, 2018). Human populations, particularly in rural areas, depend on essential ecosystem services from the natural rangeland, including food, water, medicine, recreational, aesthetic, cultural, and spiritual values (Thiaw, 2015; Ryan *et al.*, 2016). The progressive loss of biodiversity and ecosystem degradation have been increasingly scrutinized because of the high dependence of human populations on ecosystem services in Africa (Wangai *et al.*, 2016).

2.3 Droughts in South Africa

Drought is a natural hazard that is complex and is characterized by below-average rainfall beyond a specific threshold over a period of time, influencing society and ecosystems in several ways (Van Loon, 2015; Tfwala *et al.*, 2018). There are four categories of drought: hydrological, social, meteorological, and agricultural droughts. Factors that attenuate the mortality of vegetation during droughts include site characteristics, lowered competition, facilitation, attenuation of stressors and functional trait diversity in communities (Lloret *et al.*, 2012). As discussed, spatial variability in topographic and edaphic factors can generate a heterogeneous abiotic template that can result in a mosaic of drought severity across the landscape, enabling localized persistence of tree and grass populations during droughts and providing a source pool for subsequent recolonization (Lloret *et al.*, 2012).

Southern African vegetation is vulnerable to increasing temperatures as a result of climate change (Naidoo et al., 2013; Ziervogel et al., 2014). The impacts of climate change on southern African vegetation have been more pronounced in the last three decades (IPCC, 2013; King et al., 2015). Water availability also affects terrestrial species composition as some of these species have now shifted their geographic occurrence and abundance as a result of changes in species interactions associated with climate change (IPCC, 2014). The forecasted global increase in land surface temperatures is expected to be between 1.1 and 6.4 °C by the end of the century (Hui et al., 2018). This increase in temperatures is expected to affect rainfall amount and/or patterns, which in turn will lead to more rainfall variability and the occurrence of extreme precipitation events (Huntington, 2006). South Africa experienced a major drought in its summer rainfall areas peaking in 2015 and 2016. Such droughts are forecast to increase in frequency and intensity, as a result of global warming (Bond et al., 2020). Developing countries such as South Africa with scarce resources for adaption and mitigation strategies are most likely to be affected by these threats (Manabe et al., 2004). Extreme rainfall variability and events such as droughts are already evident from the reports of recorded shifts in intra-annual rainfall patterns (Knapp *et al.*, 2015).

2.4. Factors that affect Aboveground net primary production (ANPP)

2.4.1 The effect of temperature on grasses

The effect of temperature on savanna grasses is variable even under normal conditions, often characterized by pronounced dry and wet seasons (Staver *et al.,* 2011). The dry season causes rapid reductions in grass forage quality as grasses become dormant, whereas tree species tend to retain their leaves and are much more variable in their responses to rainfall seasonality (Ryan *et al.,* 2016). It is reported that the inter-annual variation of precipitation and temperature is closely related to the aboveground net primary productivity and vegetation dynamics such as plant composition and species diversity (Auerswald, 2012; Wittmer *et al.,* 2010).

Tropical savanna C4 grasses typically use water more efficiently and are more physiologically responsive to intermittent rain-fall events, compared to C3 trees and shrubs (Ghannoum *et al.*, 2003; Swemmer *et al.*, 2018; Ripley *et al.*, 2007; Ghannoum, 2009; Volder *et al.*, 2010). However, this greater water use efficiency does not necessarily translate into a greater tolerance for protracted water stress compared to C3 plants (Ghannoum, 2009; Ripley *et al.*, 2010; Volder *et al.*, 2010; Taylor *et al.*, 2011).

2.4.2 Effect of precipitation on grass productivity

Water and nitrogen are the two main factors that play vital roles in the growth of grass quality constraints. Especially in the early growing stages of grass, the amount of available water and nutrients determines the success or failure of turf establishment, time, and quality (Mobasser *et al*, 2014). Water restrictions, along with reduced nitrogen application, are the key constraints on grass growth and development and have been broadly documented to influence the leaf water relations, chlorophyll fluorescence and photosynthetic traits, which reduce plant growth performance, early senescence, and diminished crop productivity (Madani *et al.*, 2010; Mobasser *et al.*, 2014).

Vegetation productivity is projected to decline over most of southern Africa (Lawal *et al.,* 2019), with severe impacts on the structure and functioning of the savanna ecosystems (Ryan *et al.,* 2016, Osborne *et al.,* 2018). Extreme temperatures, erratic rainfall, and increasing evapotranspiration demand, coupled with the high intensity of

human activities, are likely to exceed the resilience limits of many ecosystems and trigger irreversible landscape transformation (IPCC, 2019). These impacts are particularly pronounced in southern Africa, where recent changes in climate severely affected various ecosystems and disrupted their services to society (Kusangaya *et al.*, 2014; Rosendo *et al.*, 2018).

There is evidence that change in precipitation alters natural resources such as trees and grass productivity (IPPC, 2014; Knapp *et al.*, 2015). Water availability also affects terrestrial species composition as some of these species have now shifted their geographic occurrence and abundance as a result of changes in species interactions associated with climate change (IPPC, 2014). The forecasted global increase in land surface temperatures is expected to be between 1.1 and 6.4 °C by the end of the century (Hui *et al.*, 2018). This increase in temperatures is expected to affect rainfall amounts and patterns, which in turn will lead to more rainfall variability and the occurrence of extreme precipitation events (Huntington, 2006).

2.4.3 The effect of drought and grazing on grass species and productivity

Severe droughts coupled with intense grazing can cause transitions from communities dominated by palatable, perennial grasses to systems composed of unpalatable, annual grasses and forbs (Jin *et al.*, 2018). Intense grazing can suppress grass biomass and productivity during drought years, increasing grass mortality and reducing grass basal area (Augustine and McNaughton, 2006; Swemmer *et al.*, 2018). When grazers move out of drought areas, they can also extend the ecological impacts of droughts into non-drought regions which subsequently suffer higher levels of defoliation and reductions in grass biomass (Staver, 2018).

Previous studies reported that the decline of aboveground biomass, vegetation coverage reduction, and increased soil water evaporation can be attributed to grazing intensity (Rickart *et al.*, 2013; Zhang *et al.*, 2018). These grazing effects were confirmed by several studies and demonstrated increases in soil C and N, with an increase in aboveground biomass and ground cover following the exclusion of grazing (Lu *et al.*, 2015). In other terms, the higher the production of biomass, the higher the soil content of soil organic carbon (SOC) and N. This can be attributed to the fact that the main source and pool of soil C and N is the soil organic matter (Wang *et al.*, 2012).

Therefore, lower production of biomass and lower content of N and C can be anticipated due to intensive grazing. In recent years, numerous studies have investigated drought stress on ecosystem structure and function. Yet, because of differences in the duration and intensity of drought, as well as the responding ecosystem types investigated, these experimental results are highly variable. Aboveground net primary productivity (ANPP), for example, can be reduced by extreme drought in grasslands (Beierkuhnlein, *et al.*, 2011; Hoover, *et al.*, 2014). However, other studies reported ANPP as being mostly unaffected by climate extremes (Jentsch *et al.*, 2011; Kreyling, *et al.*, 2008).

2.4.4 Previous methods used to measure drought stress

Various methods have been used to measure drought stress on ecosystem productivity, including eddy covariance techniques (Scott *et al.*, 2015), manipulative experiments (Fay *et al.*, 2000), ecosystem models (Ciais *et al.*, 2005), remote sensing (Geruo *et al.*, 2017), and in situ measurements (Munson *et al.*, 2013), or they integrated observed data with ecosystem modelling (Murray-Tortarolo *et al.*, 2016). These methods, however, have certain limitations. They are unable to monitor the drought characteristics (e.g., frequency, intensity and duration), nor can they explain the interactions with other global-change factors (e.g., elevated CO₂ concentrations, global).

2.4.5 Drought effect on grass species recovery

Indeed, many savanna ecosystems appear surprisingly resilient to moderate and even severe short-term droughts, capable of regaining productivity of both the herbaceous and woody strata within a year or two (Ruppert *et al.*, 2015; Zeppel *et al.*, 2015; Swemmer *et al.*, 2018; Fensham *et al.*, 2019). These results are indicative of the potential for high functional trait diversity in savannas and suggest that most savannas are likely to contain some species that are adapted to and can tolerate and recover from droughts (Choat *et al.*, 2012; Craine *et al.*, 2013).

Climate change is the key driver for precipitation changes which consequently impacts grassland ecosystem state, fodder output, ecological services, human society and animal productivity (Paul *et al.*, 2015). It is linked to significant physical and biological changes in ecosystems, as it is the primary determinant of where species occur, how they interact, and when biological processes occur (Bellard, 2012). Previous studies

have reported that climate change has become the leading cause of grass species diversity loss, owing to extremely amplified droughts that have been more common in the last decade (Ummenhofer and Meehl, 2017). Some studies suggest that it takes many decades for grass sward to recover from drought (O'Connor, 2015).

At present, instances of abrupt vegetation shifts following extreme droughts are rare, and most studies thus far seem to suggest that savanna and many grassland communities have the capacity to recover from periodic droughts, although recovery times can be substantial in some cases (Breshears *et al.*, 2016; Fensham *et al.*, 2019; Hoover *et al.*, 2014; Lloret *et al.*, 2012; Swemmer *et al.*, 2018).

The sustainability and productivity of the nature of grasslands mainly depend on rainfall and temperature, and these will be affected by forecasted warmer temperatures and forecasted reductions in precipitation (Volair *et al.*, 2014). When severe reduction in precipitation is accompanied by higher temperatures it is likely to lead to more frequent and intense droughts (Trnka *et al.*, 2011), which in turn will lead to plant deterioration and grassland degradation (Ciais *et al.*, 2005). Perennial forage species are the ones that are often expected to grow under reduced precipitation (Volair *et al.*, 2014). However, only plants with drought survival strategies will adapt best under rainfall reduction conditions (Norton *et al.*, 2008). It is argued that different grass species and genotypes use different strategies to tolerate and avoid drought stress as plant responses to drought are poorly understood and described (Soussana *et al.*, 2010).

Some ecological groups of grasses decrease with undergrazing or overgrazing (*referred to as decreasers*) while other grass species increase with undergrazing or overgrazing (*referred to as increasers*). The intensity of aboveground biomass harvested by animals affects the root size. Because decreasers are frequently consumed, they may have less vigor and less root biomass, which disadvantaged them in extracting soil water as compared to increaser grasses that are less grazed and thus may have well-developed root systems. It is reported that rainfall reduction also reduces decreasers and increases increasers (Magandana *et al.,* 2020). Increasers use rainfall more efficiently than decreasers due to their well-established leaf areas as a result of lower defoliation frequency and intensity associated with their lower palatability, while decreaser species, often highly palatable, are expected to

have less leaf area due to more frequent and intensive defoliation of the leaves. Hence, increasers are considered more tolerant to grazing than decreasers. Drought may lead to physiological and morphological plant modifications (Klein *et al.*, 2017). However, most genotypes that survive in many arid regions are the ones that become dormant in winter (Norton *et al.*, 2008; Norton *et al.*, 2009). Under limited resources, the growth of individual plants is also affected by the neighbouring plants (Hoover *et al.*, 2014).

Plants in arid systems survive by being tolerant to dry conditions, or by having an ephemeral life cycle, where they germinate and set seed during wet periods, thereby surviving most of the time in seed form (Whitford, 2002). Long-term droughts can, however, cause mortality in perennial species, with grasses usually being more susceptible than woody plants (van der Merwe and Milton, 2019). Severe droughts, for example, may remove trees, leading to negative effects on woody plant diversity (Swemmer et al., 2018). By reducing tree densities, droughts in savanna provide opportunities for drought-adapted flora to thrive, for instance, by promoting seedling recruitment of fast-growing, palatable shrub species and the re-establishment of a grassy layer (Swemmer *et al.*, 2018). Severe drought stress poses injurious outcomes on plant water relations, photosynthesis, ion uptake, nutrient metabolism and the partitioning of assimilates (Saud *et al.*, 2016). In this way, drought can help maintain the balance between trees and grasses (Swemmer et al., 2018).

Grasses, on the other hand, can take decades to recover their productive potential or might recover comfortably before the next drought (Swemmer *et al.*, 2018). It is also reported that there will likely be an increase in tree density and a significant decline in species richness as a result of increased temperature and rainfall variability caused by climate change (SAEON, 2015). Midgley *et al.*, (2011) also reported that most of the vegetation in the region will likely lose its capacity to tolerate drought and heat.

Ecological research in semi-arid savanna is increasingly focused on quantifying ecosystem response to global environmental change (Ruppert *et al.*, 2015; Bunting *et al.*, 2018). This research largely focuses on the consequences of severe droughts on savanna vegetation but accepts that the amplitude of observed responses would increase as droughts grow harsher and more prolonged (Ruppert *et al.*, 2015; Young *et al.*, 2017). Changes in fire regime, grazing and browsing pressure, and atmospheric

CO₂ levels can cause these savanna assemblages to alter vegetation from forest to grassland (Franco *et al.*, 2014). Long-term drought, which includes water scarcity and irregular rainfall, may result in damage of savanna rangelands (Abate *et al.*, 2016).

Different species have different strategies and adaptations to drought stress, but also different life cycle strategies (Craine *et al.*, 2012). Net primary production of many terrestrial ecosystems is limited by nitrogen availability (LeBauer and Treseder, 2008). Moreover, an increase in nitrogen availability (Taylor *et al.*, 1991). Recovery can also be slowed if frequent droughts diminish the capacity of individual plant species to replenish stored reserves, which can impact vegetation recovery through resprouting, or when it reduces seed production, impacting recovery through recolonization (Hartmann *et al.*, 2018; Ruppert *et al.*, 2015).

2.4.6 The effect of drought on the morphology of grass species

Grass leaf and stem size are affected by moisture availability and when moisture is limited, the morphological development of organs is affected negatively (Fernandez and Reynolds, 2000). Severe drought stress poses injurious outcomes on plant water relations, photosynthesis, ion uptake, nutrient metabolism, and the partitioning of assimilates (Farooq et al., 2009; Jaleel et al., 2009; Saud et al., 2013, Saud et al., 2014, Saud et al., 2016). Under drought stress, plant reactions are extremely intricate and fluctuate amongst grass species and growth phases, along with water limitation durations (Farooq et al., 2009; Fahad and Bano, 2012; Aslam et al., 2014). Nevertheless, root, and shoot growth attributes along with the leaf are significantly hampered by drought stress with an ensuing decline in the growth and development of plants (Anjum et al., 2011). The intensity of aboveground biomass harvested by animals affects the root size (Magandana et al., 2021). Because decreasers are frequently consumed, they may have less vigor and less root biomass, which makes them disadvantaged in extracting soil water as compared to increaser grasses that are less grazed and thus may have well-developed root systems. It is reported that rainfall reduction also reduces decreasers and increases increasers (Magandana et al., 2020).

2.4.7 Effect of drought on the savanna rangelands ecosystems

Savanna rangelands are less tolerant to drought and there is a high chance that increasing drought will severely impact their ecosystem functioning and maintenance

(Stuart-Haëntjens *et al.*, 2018; Cook *et al.*, 2015). Severe long-term droughts result in forb loss due to grass increase in abundance (Hoover *et al.*, 2014). The time required for restoring aspects of savanna ecosystems varies widely, ranging from less than a year (e.g., planting dominant plant species) to decades or centuries (e.g., development of plant and microbial community (Rohr *et al.*, 2018; Rydgren *et al.*, 2020; Ziter *et al.*, 2017). The full restoration of natural ecosystems is generally unachievable within periods of human study because of financial, political, and ecological constraints (Buisson *et al.*, 2019; Jones *et al.*, 2018; Rohr *et al.*, 2018; Nerlekar and Veldman, 2020).Survival of perennial grasses through droughts is not well documented but is influenced by species (du Toit, 2010; du Toit and O'Connor, 2020), duration of drought (du Toit, 2010), soil depth or rockiness (Hawinkel *et al.*, 2016), and grazing pressure (du Toit and O'Connor, 2020).

2.4.8 Grazing management strategies in communal rangelands

The management, monitoring, and interorying of plants are complicated by the diversity of plant species and the size of the ecosystem. Traditional methods of monitoring vegetation have played an important role in communal rangeland management. The information provided by these methods on biodiversity is, however, not enough (Hillebrand *et al.*, 2018). Pastoralists grazing on degraded rangelands mainly are affected by food insecurity and poverty (Donald and Jay, 2012). Although sustainable rangeland management requires ecologically sound strategies, few managers are confident that the ecology of rangeland in Southern Africa is sufficiently understood, especially within the context of balancing sustainable rangeland management with rural livelihoods (O'Connor, *et al.*, 2010).

Moderate grazing intensity is considered the basic requirement to enhance ecosystem function in grasslands (Magandana *et al.*, 2021). Yet, deterioration by overgrazing is common in many biomes, including Campos grasslands in South America. Understanding how grazing management can lead to the recovery of ecosystem function is essential to designing and implementing effective strategies for sustainable use of this resource (Fedrigo *et al.*, 2017). In semi-arid rangelands, grazing clears the grass cover, thereby, reducing grass competitive abilities with trees (Synodinos *et al.*, 2018).

2.4.9 The effect of nitrogen fertilization and drought in rangelands

Savanna grasslands are among the most widely distributed terrestrial ecosystems in the world (Dixon *et al.*, 2014). Nutrient imbalances between the vegetation and the soil are also an important factor causing grassland degradation (Shikhui *et al*, 2020). Plants match their rate of growth according to resource accessibility [for example, water, light, and nitrogen (N)] using several acclimation mechanisms. Recognizing the principal strategies and growth attributes that describe how plants respond to maximum and minimum quantities of these resources is vital for designing suitable management approaches that improve crop performance and enhance resource use efficiency in resource-restricted situations (Teixeira *et al.*, 2014). Nitrogen is an essential structural constituent of proteins, rubisco, nucleic acids, and chlorophyll in addition to some hormones, and its application in the form of fertilization is a vital agronomic management strategy to boost crop performance (Ata-UI-Karim *et al.*, 2016).

Nitrogen loading and drought stress are two important drivers in grassland ecosystems that can substantially influence the ecosystem functioning across different scales (from the single plant to the community level (Lemaire, 2012; Grant *et al.*, 2014). Nitrogen (N) fertilization increases the carrying capacity (i.e., number of animals per area) of pastures (Vasques *et al.*, 2019). In some cases, this situation creates pressure to expand grasslands and, consequently, livestock production in areas of native vegetation (Garret *et al.*, 2018). Intensification of these areas is an option to reverse the situation (Oenema *et al.*, 2014). Strategies of grassland-use intensification are expected to increase further, especially in humid and sub-humid environments (Thornton, 2010), where soil humidity is not a limiting factor for most of the year (Pandney *et al.*, 2011). One means of intensifying livestock production in grasslands is by fertilizing pastures with nitrogen (N) and optimizing the proportion of forage consumed by animals through grazing management (Lemaire, 2012).

2.4.10 Limitations and gaps in literature

A few studies dealt with the combined effect of (simulated) drought and nitrogen loading on temperate grasslands (Grant *et al.*, 2014). The interactions between these two factors, however, can be complex and are largely unknown (Lü *et al.*, 2014). There are more studies on drought, and fewer on grass recovery after long-term drought,

particularly based on species recovery. This leads to a knowledge gap on specific grass species that survive droughts as well as the management strategies to be employed after recovery. The application of nitrogen fertiliser and its effect on the recovery of the vegetation was an additional challenge encountered. The true impact of nitrogen on the recovery of grass species was diminished due to the delayed response of applied fertiliser resulting from persistent drought.

CHAPTER 3: MATERIALS AND METHODS

3.1 Study area

The study is a continuation of an existing study initiated in 2014 at the University of Limpopo experimental farm at Syferkuil in the Capricorn District Municipality of Limpopo Province, South Africa, with geographical coordinates of 23° 51' 10" S and 29° 42' 0" E (Figure 3.1).

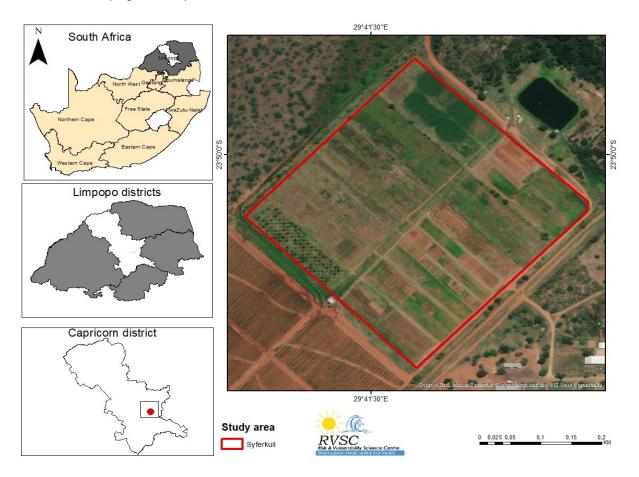


Figure 3.1 A geographical map of the Study site of the Syferkuil experimental farm, which is situated in the Polokwane municipality of South Africa (Mashala, 2023).

The climate of the research location is classified as hot arid steppe (Mujonji *et al.*, 2020) with an average annual rainfall ranging between 400 and 600 mm. According to Moshia *et al.*, (2008), the minimum and maximum temperatures in the area have a long-term average range of 4° C - 27° C, respectively. The study site is situated on a flat terrain (0 - 2% slope) at an elevation ranging from 1234 to 1240 meters above sea level (Dlamini *et al.*, 2019). The soils are primarily shallow, reddish-brown loamy sand

soils underlain by a soft plinthic B horizon and categorized as Plinthisols. The vegetation has been classified as open thorn bush savanna of the Pietersburg Plateau False Grassveld type (Acocks, 1994). Perennial C4 grasses such as *Themeda triandra, Digitaria eriantha, Schmidtia pappophoroides* and *Eragrostis* spp. dominate the herbaceous layer, whereas *Vachellia tortilis* dominates the woody component (Low and Rebelo, 1998). The investigation was conducted within a camp (or paddock) that encompassed an area of approximately 40 hectares. The experimental area is a component of a rotational camp system, which was subjected to mild grazing pressure at a stocking rate of 1 LSU ha⁻¹, where LSU represents a mature cow weighing 450 kg (Upton, 2011). The grazing regime consisted of a 30-day grazing period, followed by a 6-week interval for recovery during the growing season, and an 8-week interval during the dry season.

3.2 Experimental Setup

3.2.1 Background of the DroughtAct experiment

In 2014, a "DroughtAct" experiment was initiated to investigate the effects of extreme and ambient drought treatments with ungrazed and moderately grazed treatments. The experiment consisted of four blocks that combined drought treatments with grazing treatments, which were replicated six times, resulting in 24 plots (10 x 10 m) separated by 5 m wide corridors.

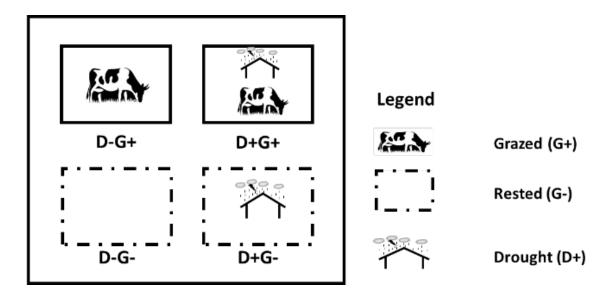


Figure 3.2 Overview of the Experimental Treatments.

Figure 3.2 illustrates the different treatments used in the previous study, including control (D-G+), resting treatment (D-G-), grazing exclusion under drought conditions (D+G-) and grazing under drought conditions (D+G+).

Permanent wire fences were used to exclude cattle from the ungrazed (G-) plots. The grazing treatment (G) was composed of two distinct levels: grazing (G+) and grazing exclusion (G-), also known as "rest." Similarly, the drought treatment comprised two levels: ambient rainfall (D-) and drought (D+) with a rainfall reduction of 66%. All four treatments were incorporated and replicated within each block, resulting in the establishment of the following combinations: resting treatment; 1) grazing exclusion under ambient rainfall conditions (D-G-), and 2) grazing exclusion under drought conditions (D+G-). Drought treatment; 3) grazing under drought conditions (D+G+), and 4) grazing under ambient rainfall conditions (D-G+: control), as illustrated in Figure 3.2.

The rainfall on the D+ plots was reduced by 66% using large rainout shelters that were constructed at the center of each plot with an area of 36 m². The shelters had a height of 2 meters and were open on all sides to allow cattle to graze and move freely underneath them. Impermeable plastic was utilized to surround the shelters and trenched to the maximum soil depth (\leq 70 cm) to prevent any lateral soil water movements from interfering. To reduce marginal effects, a central subplot of (4.8 m x 4.8 m) area was sampled and restricted in each plot.

• Drought simulation

To replicate drought conditions, 6 m x 6 m passive rainout shelters were built and fixed at locations. The design of these shelters followed that of Yahdjian and Sala (2002), but with adjustments made to their size and height to enable grazing cattle to move freely underneath. The angled roofs of the shelters were constructed from transparent polycarbonate (PC) plastic sheets, with the up-slope and down-slope roofs located at 3 m and 2 m above the ground, respectively (as shown in Figure 3.3).

Gutters and downpipes were installed on the down-slope side of the shelters to effectively drain water away from both the drought plot and its neighboring plots. These

shelters were specifically designed to decrease ambient precipitation by 66%, thereby emulating a centennial-scale drought at the study site. This corresponds to drought with a 1% probability of occurrence, based on the rainfall history of the location.

To prevent lateral soil water movements from affecting drought patches, the plots were trenched around the perimeter of the shelters to a depth of up to 70 cm and subsequently installed an impermeable plastic membrane. To minimize edge effects, a buffer of 60 cm was created between the plot's edge and the shelter, and the subplots were made smaller than the shelters (measuring 4.8 m x 4.8 m). Furthermore, the shelters were positioned in such a way as to block rain from the predominant wind direction as described by Carlyle *et al.*, (2014).

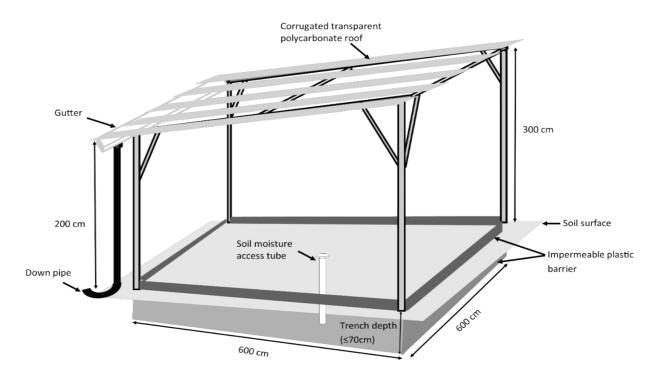


Figure 3.3 Schematic of Drought Simulation Setup.

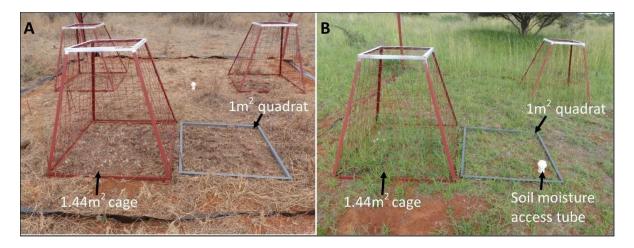
Figure 3.3 shows how drought was simulated in the experiment using a controlled setup. The transparent polycarbonate (PC) plastic sheets reduced ambient rainfall by 66% to mimic drought conditions.

• Grazing and Grazing Exclusion

In each block, a total of three long-term grazing exclosures (LTEs) were constructed, measuring 10 m x 10 m each. Two of these exclosures were subjected to drought conditions, while the third was kept under ambient conditions. These LTEs were

designed to prevent cattle grazing by utilizing five strands of high-strain wire, although they may not be completely effective in preventing game grazing. The LTEs were constructed towards the end of the 2013/2014 dry season (specifically in September/October 2014), and within each subplot, three permanent 1 m² quadrats were designated for vegetation assessment. The remaining plots in each block were divided into three under simulated drought conditions and two under ambient rainfall conditions for cattle grazing.

All plots were equipped with three sets of paired quadrats, each consisting of a 1 m² area enclosed by a 1.2×1.2 m movable short-term grazing exclosure (STE) cage and a permanent 1 m² grazed (GRA) quadrat (refer to Figure 3.4). To secure the STE cages, steel pegs were driven into the ground. Before the installation of cages, residual biomass and carryover material from the previous growing season were removed by cutting all biomass beneath the STEs down to a height of 5 centimeters, following the peak standing crop system (Ruppert and Linstädter, 2014). This ensures uniform starting points. Although the GRA was continuously grazed throughout the study period, the STE was moved around the GRA plot each season to avoid bias.



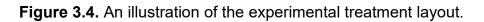


Figure 3.4 shows the arrangement of short-term ex-closure (STE) cages and grazed (GRA) quadrats in a grazed treatment under drought conditions (D+G+). Picture A was taken near the end of the 2014 growing season in October, while Picture B was taken during the 2015 growing season. The experiment was conducted by (Mudongu, 2015).

3.2.2 Current study: Post DroughtAct

The drought treatment was terminated at the end of the 2019/2020 growing season by removing the rainout shelters to investigate the effect of post-drought. The current study collected data for two growing seasons (2021 and 2022) to assess the rate of grass recovery as well as the impact of nitrogen on the rate of grass recovery after long-term drought. The nitrogen was applied during the post-drought years, 2021 and 2022. Since the current study is a component of a long-term drought project, the postdrought data (2021 and 2022 was compared with the end-of-drought data, 2020 to assess differences in the performance of grass species.

3.3 Experimental design

To address potential geographic variations, a Randomized Complete Block Design (RCBD) arranged in a Split Plot configuration, with four replications was employed. The main plot treatment comprised four drought-grazing combinations (D+G+; D+G-; D-G+ and D-G-). The subplot plot treatment involved the application of nitrogen at two levels, namely 0 and 30 kg N ha⁻¹, using Lime Ammonium Nitrate (LAN, 28% N) within each main plot treatment. This resulted in a total of eight treatments, as presented in Table 1. The main plot size was $6m \times 6m$, with a 5m-wide corridor separating the plots. A list of the different treatment combinations in addition to nitrogen fertilizer application is presented in Table 1.

| Treatments | Description |
|-------------|-----------------------------------|
| Treatment 1 | D+G+ with 0 kgN ha ⁻¹ |
| Treatment 2 | D+G+ with 30 kgN ha ⁻¹ |
| Treatment 3 | D+G- with 0 kgN ha ⁻¹ |
| Treatment 4 | D+G- with 30 kgN ha ⁻¹ |
| Treatment 5 | D-G+ with 0 kgN ha ⁻¹ |
| Treatment 6 | D-G+ with 30 kgN ha ⁻¹ |
| Treatment 7 | D-G- with 0 kgN ha ⁻¹ |
| Treatment 8 | D-G- with 30 kgN ha ⁻¹ |

| Table 1. Levels of fertilization for different treatments. |
|---|
|---|

The fertilizer treatment comprised zero fertilization (0 kgN ha⁻¹) and a minimum application of 30 kgN ha⁻¹, applied in a single dose.

3.4 Data collection

3.4.1 Aboveground Net Primary Production (ANPP)

The recovery of the herbaceous layer after drought was investigated by measuring the aboveground net primary production using both destructive and non-destructive biomass sampling methods, as described by Ruppert and Linstädter (2014). Destructive biomass sampling was conducted on the short-term grazing exclosures (STEs), while non-destructive sampling was performed through allometric calculations on the grazed (GRA) quadrats and long-term grazing exclosures (LTEs). At the beginning of the season, the STEs were cut without any sampling to eliminate any possible carry-over effects from previous seasons. To enhance the complementarity of destructive and non-destructive methods, species-specific biomass sampling was performed per quadrat along with measurements of species-specific height and cover, and then the cut biomass was dried and weighed. The plant material was dried in an oven at 60°C until a constant weight was reached and weighed accurately to the nearest gram.

The species-specific allometric equations established from the destructive biomass sampling were utilized to estimate the biomass on the GRA and LTE plots. In each season, the Short-Term Ex-closure cages were rotated within the plot to ensure that the cage production remained equal to the production that would have been achieved without the cages. The biomass sampling was conducted at the end of the growing season, which occurred from April to May each year, coinciding with the time when the majority of plant species on the plots had reached their full growth and flowering stages. During the peak biomass season, the cutting and sampling of biomass were performed on a per-quadrat and per-species basis.

To evaluate the recovery rate of herbaceous species, vital rates including height, growth stage, and chlorophyll content were monitored. The effects of treatments on the herbaceous layer were determined to identify the species that were exhibiting recovery and those that were not. To minimize the impact of destructive sampling on monitoring plots, a total of three sampling quadrats (50 x 50 cm) per plot were used to collect ANPP in ungrazed plots. In grazed plots, standing biomass was collected in

three 1m² quadrats protected from grazing by STE movable cages, as described by Linstädter *et al.*, (2013). Prior to biomass harvesting, the species identity, average height of five individuals, predominant phenology, and the computed percentage of total canopy cover for each species were determined. In addition, the canopy cover was classified into living material comprising both green and senescent parts and standing dead material, which refers to the previous year's grey and oxidized plant material. Moreover, the percentage of litter, bare ground, and other materials such as manure and stones were estimated at the quadrant level.

3.4.2 Plant Functional Types

Description of Plant Functional Types (PFTs)

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

- (i) Annual grasses (Annual)
- (ii) Narrow-leaved perennial grasses (Hglin)
- (iii) Broad-leaved perennial grasses (Hglan)
- (iv) Very-broad-leaved perennial grasses (Hgova)

These traits relate to life history, growth form and leaf width. 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).

3.5 Data analysis

Descriptive statistics such as mean was carried out using Microsoft Excel. Differences in species composition, aboveground net primary production (ANPP) and plant functional type were assessed through standard analysis of variance (ANOVA) using Statistix 10 software. In cases where the treatment means were significantly different, a mean separation was carried out using the Duncan multiple range test at a 5% probability level of testing ($P \le 0.05$).

CHAPTER 4: RESULTS

4.1 Weather variable during the growing season

The diagram presented in Figure 4.1 illustrates the observed precipitation and temperature patterns at the study location subsequent to the drought period. Within the context of the drought experiment, meteorological factors, specifically temperature had a significant impact on the recovery of grass species after the elimination of the drought factor. Temperature influences essential physiological processes in plants, such as photosynthesis and respiration, which can impact their growth and yield.

The analysis of the temperature data patterns over the years following the drought was conducted. During the first year, 2021 following drought, a spectrum of temperatures ranging from 7.01 °C to 35.74 °C was recorded. In the second year, a temperature range spanning from 7.01 °C to 32.23 °C was recorded. The temperature ranges indicate a decrease in the highest recorded temperature in the first year after the drought. The observed change might potentially suggest a cooling trend, which may have ramifications for the regeneration of grass species. This shift could influence many plant physiological aspects, including evapotranspiration and the level of water stress experienced by plants.

In the third year, 2023, following the drought, the recorded temperatures varied between 16.03 °C and 29.82 °C. Although the temperature range observed in this year is slightly narrower, it nevertheless includes a diverse spectrum. The observed reduction in temperature variability during the third year following the drought event may suggest an enhanced level of temperature stability, potentially influencing the adaptive and recovery mechanisms of plants. The analysis of temperature data patterns provides significant insights into the ecological conditions following a drought event and their possible impact on the recovery of grass species. The consequences of the observed temperature pattern alterations on the processes driving vegetation response to the elimination of drought will further be investigated in the following sections.

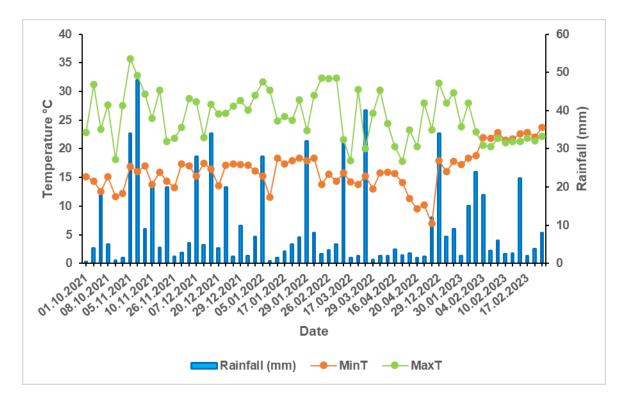


Figure 4.1 Rainfall and Temperature Trends in the Study Area (2021-2023).

4.2 Plant functional types occurrence

Table 4.1 presents the prevalence and variability of PFTs, emphasizing key species and their adaptability in response to grazing, drought, and historical treatment conditions.

4.3 Overall cover and occurrence of PFTs and species within the study area

The analysis incorporates a thorough comparison among various Plant Functional Types (PFTs), unravelling patterns of occurrence across distinct treatments and growth seasons. Within this framework, the most prevalent PFTs and their representative species are highlighted, providing insights into the ecological dynamics (Table 4.1).

Among annual grasses, a consistent presence is observed, with notable peaks in the drought-history treatments (D+G+) during 2021, signifying resilience to grazing and drought-history. Broad-leaved grasses (HG lan) exhibit *Aristida congesta* as a

predominant species, showcasing its persistent occurrence across treatments and years. *Aristida stipitata* and *Schmidtia pappophoroides* also emerge as influential contributors within narrow-leaved grasses (HG lin), illustrating their adaptability.

Within very-broad-leaved grasses (HG ova), *Digitaria eriantha* consistently contributes, emphasizing its adaptability across different conditions. This comparison across PFTs underscores the dominance of broad-leaved grasses, with *Aristida congesta* being the most recurrent species, signifying its ecological significance.

In addition to highlighting the most common occurrences, it is imperative to identify the least occurring PFTs and their representative species to comprehend the overall biodiversity and ecosystem dynamics comprehensively. This detailed examination provides a nuanced understanding of the intricate relationships among different PFTs, contributing to a more holistic interpretation of the vegetation dynamics under varying environmental conditions.

Moreover, the analysis unveils the least occurring PFTs and their associated species, shedding light on the less dominant components within the vegetation. Notably, within the annual grasses plant functional group, *Bulbostylis hispidula* emerges as one of the least occurring PFTs, with minimal representation in both grazed and ungrazed conditions across the years.

Within narrow-leaved grasses (HG lin), species like *Aristida diffusa* and *Chloris virgata* exhibit comparatively lower occurrences, indicating their reduced prevalence in the studied conditions. *Dactyloctenium aegyptium* and *Dactyloctenium giganteum*, among the annual grasses, showcase limited presence, emphasizing their vulnerability or specific ecological niche requirements.

The identification of the least occurring PFTs and their associated species contributes essential information to the ecological narrative. It allows for a nuanced understanding of biodiversity distribution and potential indicators of environmental sensitivity. Integrating these insights enriches the ecological interpretation, providing a comprehensive overview of the plant community dynamics within the DroughtAct experiment, within different treatments and across different years.

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Table 4.1: The number of Plant Functional Types (PFTs) over time and associated species across different treatments and growth seasons in the DroughtAct experiment.

| | D+ | -G- | | | Tot al | D+G+ | | | Total | D-G- | | | Total | D-G+ | | | Total | Grand Total |
|--------------------------------|---------------|-----|------|------|-----------|------|------|------|-------|------|------|------|-------|------|------|------|-------|----------------|
| | | 020 | 2021 | 2022 | | 2020 | 2021 | 2022 | | 2020 | 2021 | 2022 | | 2020 | 2021 | 2022 | | |
| Annual | | 1 | 7 | 2 | 10 | 10 | 17 | 8 | 35 | 2 | 3 | 4 | 9 | 7 | 8 | 8 | 23 | 7 |
| Bulbostylis hispidula | | | | | | | | 7 | 7 | | | 3 | 3 | | | 5 | 5 | |
| Dactyloctenium aegyptium | | | 1 | | 1 | 5 | 5 | | 10 | | | | | | 1 | | 1 | |
| Dactyloctenium giganteum | | | | | | | 8 | | 8 | | | | | 2 | | | 2 | |
| Kyllinga alba | | | | 2 | 2 | | | | | | | | | | 1 | 2 | 3 | |
| Melinis repens | | 1 | 4 | | 5 | 1 | 1 | 1 | 3 | 2 | 3 | 1 | 6 | 4 | 4 | 1 | 9 | : |
| Trag.bert | | | 2 | | 2 | 4 | 3 | | 7 | | | | | 1 | 2 | | 3 | |
| HG lan = broad-leaved grasses | | 10 | 17 | 17 | 44 | 27 | 40 | 36 | 103 | 24 | 31 | 19 | 74 | 64 | 48 | 23 | 135 | 3 |
| Aristida congesta | | | 6 | 5 | 11 | 9 | 12 | 14 | 35 | 4 | 6 | 4 | 14 | 12 | 12 | 9 | 33 | |
| Brachiaria negropedatata | | 1 | 1 | 1 | 3 | 2 | 4 | 3 | 9 | 2 | 3 | | 5 | 9 | 7 | 3 | 19 | |
| Eragrostis rigidior | | | | | | | | 1 | 1 | | | | | | | | | |
| Eragrostis superba | | | | 2 | 2 | 1 | 3 | 3 | 7 | | | | | 5 | 4 | | 9 | |
| Heteropogon conturtus | | 2 | 1 | 2 | 5 | 1 | 2 | 1 | 4 | 5 | 5 | 5 | 15 | 9 | 5 | 2 | 16 | |
| Pogonarthria saquarrosa | | | | | | 2 | 4 | | 6 | | 3 | | 3 | 8 | 4 | | 12 | |
| Schmidtia pappophoroides | | 7 | 9 | 7 | 23 | 10 | 12 | 12 | 34 | 11 | 12 | 8 | 31 | 9 | 9 | 8 | 26 | 1 |
| Themeda triandra | | | | | | 1 | 2 | 2 | 5 | 1 | 2 | 2 | 5 | 2 | 6 | 1 | 9 | |
| Trichoneura. grandiglumis | | | | | | | | | | | | | | 7 | 1 | | 8 | |
| Tricholaena monachne | | | | | | 1 | 1 | | 2 | 1 | | | 1 | 3 | | | 3 | |
| HG lin = narrow-leaved grasses | | 7 | 20 | 23 | 50 | 17 | 42 | 50 | 109 | 16 | 22 | 21 | 59 | 26 | 33 | 33 | 92 | 3 |
| Aristida diffusa | | 1 | 2 | 6 | 9 | 1 | 7 | 12 | 20 | 2 | 3 | 2 | 7 | 9 | 10 | 8 | 27 | |
| Aristida stipitata | | 3 | 6 | 6 | 15 | 11 | 12 | 10 | 33 | 7 | 8 | 7 | 22 | 12 | 12 | 9 | 33 | 1 |
| Chloris virgata | | | | 1 | 1 | | 3 | 4 | 7 | | | 1 | 1 | 1 | 2 | 1 | 4 | |
| | Dicoma toment | osa | 1 | | 1 | | | | | | | | | | | | | |

| | | | | 1 | 1 | | 2 | | | | | | | | | 2 |
|---|------------------|-------------------------|-----|--|--|---|---|--|--|--|--|--|--|---|---|---|
| | | | | | | | | 1 | 1 | | 2 | | | | | 2 |
| 1 | | 1 | : | 3 | 6 | 4 | 13 | 11 | 8 | 3 | 22 | 11 | 10 | 4 | 25 | 62 |
| 1 | | 1 | : | 4 | 7 | 4 | 15 | 12 | 9 | 3 | 24 | 11 | 10 | 4 | 25 | 66 |
| | | | 1 | | 2 | 4 | 6 | | 1 | 1 | 2 | | 3 | 6 | 9 | 18 |
| | | 1 | | | | | | | | | | | | | | 1 |
| 2 | | 3 | ł | ; | 2 | | 2 | 1 | 3 | | 4 | | | | | 11 |
| | | 1 | | | | | | | | | | | | | | 1 |
| 1 | | 6 | 8 1 | 4 | 11 | 12 | 27 | 6 | 6 | 6 | 18 | 4 | 5 | 6 | 15 | 75 |
| | | | 1 | 1 | 5 | 8 | 14 | | 1 | 4 | 5 | | 1 | 3 | 4 | 24 |
| | 1 2 1 1 | 1 2 <u>1</u> 1 | 1 | 1 6 8 15 1 1 2 3 5 1 1 1 1 1 1 1 2 | 1 1 2 3 5 1 1 1 1 1 1 1 2 4 | 1 6 8 15 4 11 1 1 1 1 2 2 3 5 2 1 1 1 1 1 1 2 2 3 1 1 2 1 1 1 1 2 2 1 1 2 2 1 1 1 2 2 1 | 1 6 8 15 4 11 12 1 1 1 1 1 12 2 3 5 2 1 1 1 1 1 1 1 1 1 2 4 1 1 1 2 4 1 1 2 4 1 | $ \begin{array}{c ccccccccccccccccccccccccccccccccccc$ | $ \begin{array}{c ccccccccccccccccccccccccccccccccccc$ | 1 6 8 15 4 11 12 27 6 6 1 1 1 1 1 12 27 6 6 2 3 5 2 2 1 3 1 1 15 2 2 1 3 1 1 1 2 4 6 1 1 1 1 2 4 6 1 1 1 2 4 7 4 15 12 9 1 1 2 3 6 4 13 11 8 1 1 2 3 6 4 13 11 1 | $ \begin{array}{c ccccccccccccccccccccccccccccccccccc$ | $ \begin{array}{c ccccccccccccccccccccccccccccccccccc$ | $ \begin{array}{c ccccccccccccccccccccccccccccccccccc$ | 1 6 8 15 4 11 12 27 6 6 6 18 4 5 1< | 1 6 8 15 4 11 12 27 6 6 6 18 4 5 6 1< | 1 6 8 15 4 11 12 27 6 6 6 18 4 5 6 15 1 |

4.4. Aboveground Net Primary Production: Final year of drought vs. Post-drought years

In this analysis (Figure 4.2), the intricate dynamics of Aboveground Net Primary Production (ANPP) within the context of the Drought-Act experiment, which unfolded over six years, commencing in 2015 and culminating in 2020 was investigated. This experimental setup subjected the study area to a protracted drought simulation, offering a unique opportunity to explore the impact of this extended dry period on ecosystem productivity. The specific focus of the current study, however, centred on the terminal year of the long-term drought experiment, 2020, and contrasts it with the nascent stages of recovery observed in 2021 and 2022.

One of the salient findings that emerged from this investigation revolves around the pivotal role of grazing in shaping ANPP dynamics. The final year of the drought (2020) revealed a notable reduction in ANPP, a trend that was consistent across both drought (D+) and non-drought (D-) conditions when grazing was introduced (G+). This suggests that the influence of grazing intensified the reduction in ANPP during the drought's culmination. This was particularly evident when contrasting ANPP in 2020 with the ensuing recovery years. When drought conditions persisted and grazing was absent (G-), ANPP exhibited a substantial decline in the last year of the drought (2020) in comparison to the early years of recovery (2021 and 2022). This decline underscores the lasting impact of drought on ANPP, even after the drought subsided, particularly when grazing pressure was low.

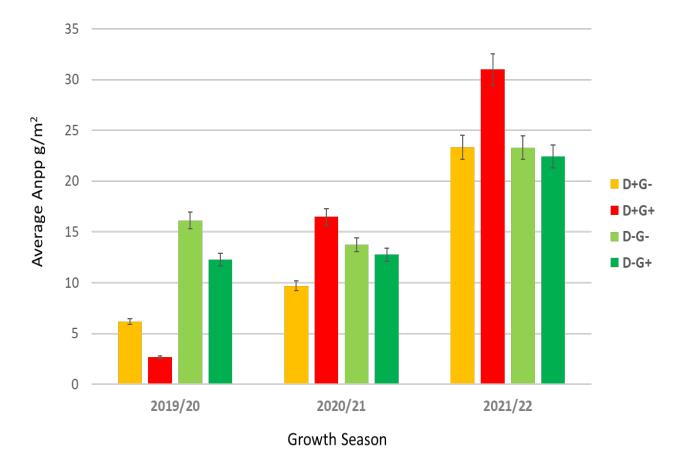
Notably, under ambient conditions, the ANPP observed in the final year of long-term drought in 2020 exhibited a resemblance to the levels witnessed during the initial phases of recovery in 2021 and 2022. This unexpected phenomenon, irrespective of grazing's presence, suggests a potential resilience within the ecosystem.

When contrasting non-drought conditions (ambient settings), a pattern emerged that was distinct from the drought's impact. It was evident that ANPP during the final drought year (2020) showed an alignment with the recovery phases, whether grazing was a factor or not. Furthermore, the subsequent recovery years (2021 and 2022)

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demonstrated a noteworthy resurgence in ANPP, especially under grazed conditions. This resurgence points to the influential role of grazing in stimulating ANPP during the recovery phase. These ANPP dynamics are visually represented in Figure 4.2, offering a comprehensive overview of the interactions between drought, grazing, and ANPP.

This detailed interpretation underscores the multifaceted interplay between environmental stressors, grazing, and ecosystem resilience. It unravels the complex responses of ANPP to drought, offering valuable insights into the lasting impact of drought on ecosystem productivity and the potential for recovery, notably under the influence of grazing.



Treatments: Anpp production over time

Figure 4.2 Aboveground Net Primary Productivity (ANPP) Trends in the Final Year of Drought (2020) Compared to Initial Recovery Years (2021-2022) Under Different Treatments.

4.5 Biomass Production and Plant Functional Types (PFTs):

The assessment of biomass production across various Plant Functional Types (PFTs) under different treatments during the final year of drought and the ensuing postdrought years revealed a multitude of intriguing relationships and dynamics (Figure 4.3). Statistical analysis indicated the presence of highly significant differences in biomass production across these treatments (P = 0.0001). These differences, however, were not uniform and exhibited a distinct dependency on the specific treatment combinations, pointing to the subtle interplay between environmental factors and PFT performance.

4.6 Plant Functional Type (PFT) Ranking and Recovery Rates:

Remarkably, the results consistently proved the dominance of broad-leaved and narrow-leaved grasses in biomass production across all treatment combinations. These PFTs not only exhibited higher productivity but also displayed noteworthy resilience and rapid recovery capabilities in the post-drought years. The prominence of these PFTs across treatments underlines their ecological significance and the adaptive strategies they employ to thrive in varying environmental conditions (Figure 4.3).

4.7 Biomass Dynamics under Drought and Non-Drought Conditions:

Significantly, biomass production exhibited substantial fluctuations when subjected to drought conditions, contrasting with more stable outcomes in non-drought settings. This difference reflects the expected effects of prolonged drought on primary production, where environmental stressors challenge plant growth and productivity. However, as anticipated, the final year of the long-term drought in 2020 resulted in lower biomass production compared to post-drought phases, signifying the system's response to the release of stress and the gradual restoration of productivity (Figure 4.3).

4.8 Biomass Production under Grazed and Ungrazed Conditions:

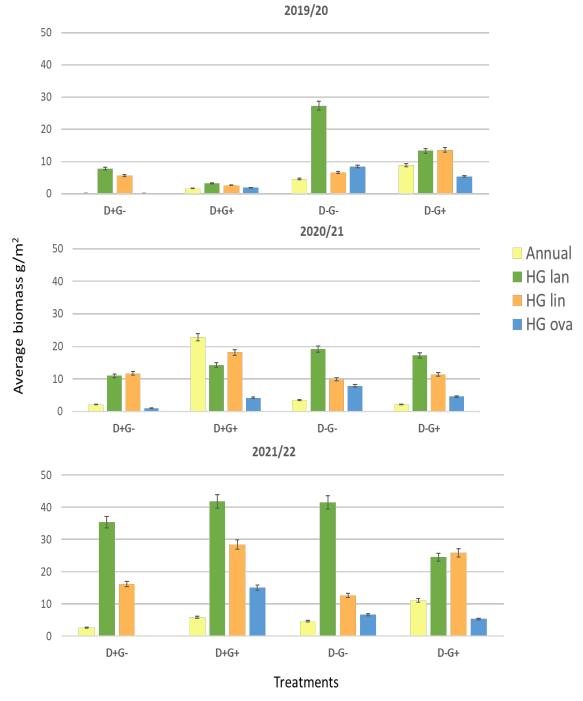
An insightful observation emerged from the analysis of biomass production under grazed and ungrazed conditions (Figure 4.3). Ungrazed vegetation displayed higher variability in biomass production, suggesting the profound influence of herbivory on plant growth and inter-species competition. Notably, the last year of drought (D+G-) recorded the lowest biomass production, where two PFTs, annuals and very broad-leaved grasses, were significantly impacted, indicating their susceptibility to combined stressors.

4.9 Dynamic Changes in PFT Dominance:

The final year of the drought experiment revealed a substantial decline in the biomass production of all PFTs (Figure 4.3). In particular, very broad-leaved grasses and annuals experienced marked reductions in primary production during this period. However, as the ecosystem transitioned into the first year post-drought, a general improvement in biomass production was observed across all PFTs, reflecting the initial stages of ecological recovery. Remarkably, in the first year post-drought, narrow-leaved grasses and annual grasses emerged as the highest producers under drought-history treatments, showcasing their capability to capitalize on the alleviation of stress and resource competition.

In the second growth season post-drought, a noticeable shift in PFT dominance was observed. Broad-leaved grasses assumed the role of the highest biomass producers in drought-history treatments (D+G- and D+G+), followed closely by narrow-leaved grasses. This shift underscores the dynamic nature of PFT interactions within ecosystems, as different species adjust to changing conditions and resource availability. Importantly, the findings suggested that under drought-history treatments, grazed vegetation displayed slightly higher primary production. This emphasizes the role of herbivory in shaping biomass dynamics, illustrating its influence on the composition and productivity of plant communities.

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PFTs Biomass Production over time

Figure 4.3 Variation in plant functional types (PFTs) biomass production during drought and post-drought years.

Annual = annual grasses, HG lan = broad-leaved grasses, HG lin = narrow-leaved grasses, and HG ova = very-broad-leaved grasses.

4.10 The impact of grazing (G+ vs. G-) on biomass production of PFTs under drought conditions

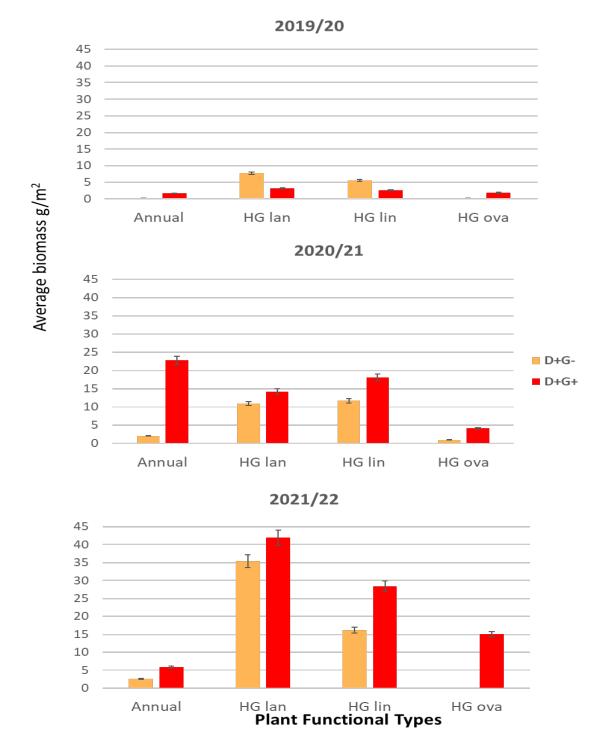
Figure 4.4 presents the dynamics of biomass production among distinct Plant Functional Types (PFTs) under the influence of grazing (G+ vs. G-) within both drought and drought-history treatments across various growth seasons.

In the functional group of annual grasses (Annual), a consistent trend unfolds, revealing higher biomass production under grazing conditions (G+) across growth seasons, with the pinnacle observed in the 2020/21 season. Broad-leaved grasses (HG Ian) exhibit a pattern of higher biomass under the ungrazed treatment (G-) during the 2019/20 season, followed by a reversal in subsequent seasons, where grazed conditions (G+) manifest higher biomass.

Narrow-leaved grasses (HG lin), displayed a variable response to grazing. While G+ produced higher biomass in the 2020/21 and 2021/22 seasons, the 2019/20 season resulted in comparable or slightly higher biomass under ungrazed conditions (G-). Very-broad-leaved grasses (HG ova), however, consistently display higher biomass production under grazing conditions (G+) throughout all growth seasons, portraying a positive correlation between grazing and increased biomass.

Comparing across different growth seasons, the 2019/20 season demonstrates variable responses to grazing, with positive effects on annual grasses and very-broad-leaved grasses. The 2020/21 season witnesses an overall increase in biomass production, notably influenced by grazing in all PFTs, particularly, annual grasses and narrow-leaved grasses. Similarly, the 2021/22 season displayed an overall increase in biomass production in response to grazing, emphasizing the positive impact of grazing on the growth of herbaceous species.

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PFTs Biomass Production: Grazing vs. Non-grazing

Figure 4.4 The figure presents a comparative analysis of the impact of grazing (G+ vs. G-) within drought and drought-history treatments on the biomass production of the four distinct Plant Functional Types (PFTs).

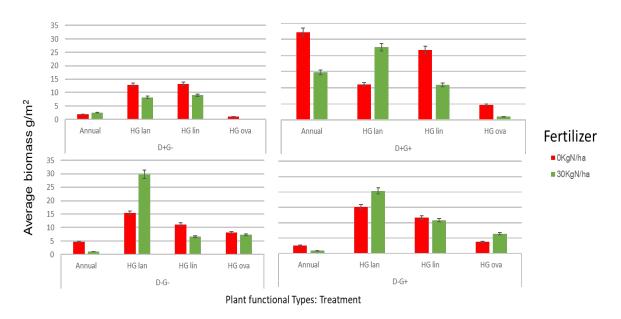
Annual = annual grasses, HG lan = broad-leaved grasses, HG lin = narrow-leaved grasses, and HG ova = very-broad-leaved grasses.

4.11 Nitrogen fertilizer effect on primary production of Plant Functional Types (PFTs)

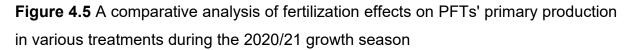
Figure 4.5 reveals distinct patterns in biomass production across different treatments and fertilization levels. Under the D+G- treatment, a notable increase in biomass production is observed specifically for Annual grasses at 30 kgN/ha, suggesting a positive response to higher nitrogen levels in this particular PFT. However, all the other PFTs had higher biomass production at 0 kgN/ha.

In the D-G- treatment, the increase in biomass production was specifically observed in broad-leaved grasses (HG Ian), while other PFTs experienced the opposite, indicating a mixed response to fertilization within this treatment. Focusing on the D+G+ treatment, the increase in biomass production was only observed in the broad-leaved grasses. Lastly, under the D-G+ treatment, the increase in biomass production is observed for both HG Ian and HG ova, indicating a dual positive response within these plant functional types to elevated nitrogen levels.

In summary, the observations highlight specific PFTs within each treatment that exhibit increased biomass production in response to fertilization, showcasing the nuanced impact of nitrogen levels on different plant functional types across treatments. Overall, the effect of fertilizer was generally not realized across the various treatments.



PFTs Biomass Production: Fertilized vs. Unfertilized Growth season: 2020/21



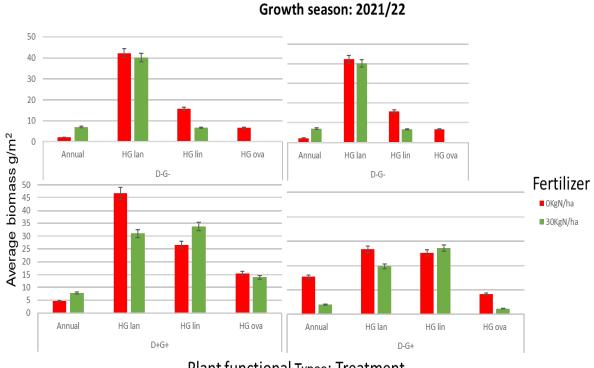
Annual = annual grasses, HG lan = broad-leaved grasses, HG lin = narrow-leaved grasses, and HG ova = very-broad-leaved grasses.

In the growth season of 2021/22, the biomass production dynamics of different Plant Functional Types (PFTs) were assessed under various treatments, focusing on the influence of nitrogen levels (0 kgN/ha vs. 30 kgN/ha) (Figure 4.6).

A similar, inconclusive, response to fertilization was observed in the second growth season post-drought. Within the D+G- treatment, annual grasses and narrow-leaved grasses exhibited a substantial increase in biomass production at 30 kgN/ha. It was also observed that no very-broad-leaved grasses were found in this treatment. Under the D-G- treatment, only Annual grasses displayed increased biomass production at 30 kgN/ha. All other PFTs within this treatment showcased decreased biomass production with increased nitrogen. In the D+G+ treatment, annual grasses and narrow-leaved grasses (HG lin) exhibited heightened biomass production at 30 kgN/ha, while the other PFTs showed a decreased biomass production. A similar pattern is observed under the D-G+ treatment, where two PFTs, only narrow-leaved

grasses, displayed increased biomass production at 30 kgN/ha, while the remaining PFTs declined in biomass production.

Overall, similar to the 2020/21 growth season, the examination of each PFT's response to varying nitrogen levels within different treatments reveals contrasting and inconclusive effects of fertilization on biomass production.



PFTs Biomass Production: Fertilized vs. Unfertilized Growth season: 2021/22

Plant functional Types: Treatment

Figure 4.6 A comparative analysis of fertilization effects on PFTs' primary production in various treatments during the 2021/22 growth season.

Annual = annual grasses, HG lan = broad-leaved grasses, HG lin = narrow-leaved grasses, and HG ova = very-broad-leaved grasses.

CHAPTER 5: DISCUSSION

5.1 Recap of Key Findings

This study investigated the complex interactions between prolonged drought, grazing, and nitrogen fertilization on herbaceous species in a semi-arid savanna ecosystem. The key findings of the study can be summarized as follows:

- Prolonged drought significantly reduced aboveground net primary production (ANPP) and biomass production of herbaceous species, highlighting the negative impact of drought stress on plant productivity.
- Grazing played a dual role in influencing plant productivity, intensifying ANPP reduction during the final drought year but stimulating biomass production during recovery phases. This suggests that grazing can be a useful tool for promoting plant recovery from drought, but careful management of grazing intensity is essential to avoid overgrazing.
- The impact of nitrogen fertilization on biomass production was nuanced and varied across plant functional types (PFTs), emphasizing the need for a more targeted approach to nitrogen fertilization in semi-arid savanna ecosystems.

The identification of dominant and least occurring PFTs provides valuable insights into biodiversity distribution and informs conservation efforts to maintain the functional diversity of semi-arid savanna ecosystems.

5.1.1 Weather Variables and Plant Responses

This study observed a potential cooling trend in temperature patterns post-drought, which may have influenced plant physiological processes. This finding aligns with previous studies that have documented the influence of temperature fluctuations on plant growth and productivity in semi-arid ecosystems (Luo *et al.*, 2011; Xu *et al.*, 2015) The observed temperature stability in the third post-drought year may have further influenced plant adaptive mechanisms, allowing for the gradual recovery of plant communities from drought stress. In contrast to a previous study reported by (Aslam

et al., 2020), reported that temperature fluctuation increases the forward and reverse biochemical reactions exponentially resulting in the denudation of enzymes, and depending on the intensity or duration of temperature reversible or irreversible may lead to plant death.

5.1.2 Plant Functional Types Composition and Biodiversity

The dominance of broad-leaved and narrow-leaved grasses, particularly *Aristida congesta*, across treatments and years highlights the resilience of these PFTs under varying environmental conditions. This finding is consistent with previous studies that have identified these PFTs as prevalent in semi-arid savanna (Eldridge *et al.*, 2011). The identification of least occurring PFTs and species contributes to understanding biodiversity distribution and provides valuable insights for conservation efforts.

5.1.3 Aboveground Net Primary Production (ANPP) and Drought Recovery

The observed reduction in ANPP during the final drought year (2020) emphasizes the negative impact of prolonged drought on plant productivity. This finding is consistent with numerous studies that have documented the detrimental effects of drought on ANPP in semi-arid ecosystems (Nippert and Knapp, 2004; Zhou *et al.*, 2016).

The result contrasts with the outcomes of the previous study (Denton *et al.,* 2014), which indicated that drought did not significantly reduce ANPP.

The persistence of lower ANPP values even after the drought has subsided suggests the lingering effects of drought stress on plant physiological processes and resource availability. The findings correlate with previous studies that have indicated under drought conditions the physiological process slows down (Aliyeva *et al.,* 2023).

The positive correlation between grazing and ANPP during recovery phases highlights the potential role of grazing in promoting plant productivity in semi-arid savanna ecosystems. This finding aligns with previous studies that have shown that grazing can stimulate plant growth and nutrient cycling under certain conditions (Behnke *et al., 1993;* Milchunas *et al., 2001*). However, the impact of grazing on plant productivity could also be influenced by microclimatic variations, particularly in association with grazing intensity and herbivore movement patterns. This observation highlights the

need to recognize the importance of grazing intensity and timing in veld management to avoid overgrazing and its associated negative impacts.

5.1.4. Impact of Grazing and Nitrogen Fertilization on PFT Biomass

The observed increase in biomass production of certain PFTs under grazing, particularly annual grasses and very-broad-leaved grasses, suggests that grazing can have a positive impact on plant productivity in specific functional groups. This finding is consistent with previous studies that have documented differential responses of PFTs to grazing pressure (Briske *et al.*, 2006; Bardgett *et al.*, 2011). However, the observed increase in biomass production of certain PFTs under grazing could also be attributed to herbivore preferences, suggesting that grazing may promote the dominance of more palatable or less preferred species. The higher biomass variability in grazed vegetation compared to ungrazed vegetation indicates the influence of herbivory on plant growth dynamics and the potential for grazing to promote plant diversity.

The impact of nitrogen fertilization on biomass production was found to vary across PFTs, with some PFTs showing increased biomass while others showed no significant response. This finding is consistent with previous studies that have documented the complex and often context-dependent effects of nitrogen fertilization on plant productivity in semi-arid ecosystems (Throop *et al.*, 2004; Gill *et al.*, 2002). The nuanced impact of nitrogen levels on different PFTs emphasizes the need for a more targeted approach to nitrogen fertilization in semi-arid savanna ecosystems, considering PFT composition and environmental factors. Moreover, the inconclusive responses of PFTs to nitrogen fertilization could be attributed to indirect effects, such as changes in soil microbial communities or nutrient cycling dynamics.

5.1.5 Theoretical Frameworks

The findings of this study align with several theoretical frameworks, including the following, which have been proposed to explain the interactions between environmental stressors, management interventions, and plant responses in semi-arid ecosystems.

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- The Non-Equilibrium Paradigm (NEP) suggests that semi-arid ecosystems are characterized by high variability and frequent disturbances, such as drought, which drive plant community dynamics and limit plant productivity (Noy-Meir, 1975). The observed reduction in ANPP and biomass production during drought periods in the present study is consistent with this framework.
- The Plant-Herbivore Hypothesis proposes that grazing can have both positive and negative impacts on plant productivity, depending on the intensity, timing, and selectivity of grazing (McNaughton, 1983). The findings of the present study, which showed that grazing intensified ANPP reduction during drought but stimulated biomass production during recovery, support this hypothesis.
- The Resource-Limitation Hypothesis suggests that plant productivity in semiarid ecosystems is often limited by the availability of essential resources, such as water and nitrogen (Aerts *et al.*, 1999). The observed variability in nitrogen fertilization responses across PFTs in the present study highlights the complex interactions between plant nutrient requirements and nitrogen availability in these ecosystems.

CHAPTER 6: CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

This dissertation examined the impact of prolonged drought, moderate grazing, and nitrogen fertilization on the recovery of herbaceous species in a semi-arid savanna ecosystem. The study focused on aboveground net primary production (ANPP) and standing biomass yield as indicators of plant productivity. The findings highlight the need for a holistic and adaptive approach to ecosystem management that considers the combined effects of these factors on plant communities and ecosystem resilience. Future research should focus on long-term monitoring, spatial expansion, and targeted management strategies to further enhance our understanding and conservation of these vital ecosystems.

One of the key findings is that prolonged drought significantly reduced both ANPP and biomass production of herbaceous species. This emphasizes the negative impact of drought stress on plant productivity. The persistence of lower ANPP values even after drought subsides suggests the lingering effects of drought stress on plant physiological processes and resource availability. These findings highlight the need for careful management of water resources and drought mitigation strategies to protect semi-arid savanna ecosystems from the detrimental effects of prolonged drought.

The impact of grazing on plant productivity was nuanced and varied across years and plant functional types (PFTs). Grazing intensified ANPP reduction during the final drought year but stimulated biomass production during the recovery phases. This suggests that grazing can have a dual role in influencing plant productivity, depending on the timing and intensity of grazing. Careful management of grazing intensity and timing is crucial to avoid overgrazing and its associated negative impacts, while also harnessing the potential of grazing to promote plant recovery from drought.

The impact of nitrogen fertilization on biomass production also varied across PFTs, with some PFTs showing increased biomass while others showed no significant response. This finding emphasizes the need for a more targeted approach to nitrogen fertilization in semi-arid savanna ecosystems. Nitrogen fertilization rates, timing, and forms of application should be considered relative to PFT composition and

environmental factors to optimize nitrogen fertilization strategies and minimize potential negative impacts.

6.2 Answers to Objectives

Objective 1: Assessing the recovery of grass species

The study evaluated aboveground net primary production (ANPP) and standing biomass yield as indicators of grass species recovery after long-term drought and moderate grazing. The following observations were made:

- PFTs responded differently to the release of drought, depending on whether there was grazing or not. Under grazed conditions, annual and narrow-leaved grasses were the first PFTs to show signs of recovery. Whereas, under nongrazed conditions, broad-leaved and narrow-leaved grasses performed better.
- Furthermore, prolonged drought significantly reduced both ANPP and biomass production, highlighting the negative impact of drought stress on plant productivity.
- A subtle response to grazing, with grazing intensifying ANPP reduction during the final drought year but stimulating biomass production during recovery phases.

Objective 2: Examining the impact of nitrogen fertilization

The study investigated the impact of a minimal dose of nitrogen fertilization on grass species and biomass production after combined long-term drought and moderate grazing. The following observations were made:

 The findings indicated that the impact of nitrogen fertilization varied across plant functional types (PFTs), with some PFTs showing increased biomass while others showed no significant response. Overall, nitrogen fertilization had an inconclusive impact on the biomass production of PFTs and grass species in the recovery years.

6.3 Implications for future research

This study provides a valuable foundation for addressing critical knowledge gaps in the understanding of plant responses to environmental stressors and management interventions in semi-arid savanna ecosystems.

6.4 Recommendations for Practice

The findings of the present study suggest several practical recommendations for managing semi-arid savanna ecosystems to promote plant productivity, resilience, and biodiversity:

- Adaptive Grazing Management: Implement adaptive grazing strategies that adjust grazing intensity, timing, and selectivity in response to environmental conditions, particularly drought. During drought periods, reducing grazing pressure can help minimize the negative impacts of drought on plant productivity and allow for more rapid recovery.
- 2) Precision Nitrogen Fertilization: Employ precision nitrogen fertilization techniques that target specific plant functional types (PFTs) based on their nutrient requirements and responses. This will optimize nitrogen use efficiency, maximize plant productivity, and minimize potential environmental impacts.
- 3) Monitoring and Adaptive Management: Implement a comprehensive monitoring program to track plant productivity, species diversity, and ecosystem health in response to management interventions. Use this information to adapt grazing and nitrogen fertilization strategies as needed to ensure long-term ecosystem sustainability.

- 4) Conservation of Less Common PFTs: Implement targeted conservation measures to protect less common PFTs, which despite their lower abundance, contribute significantly to functional diversity and ecosystem resilience. This could include establishing protected areas, implementing habitat restoration efforts, and educating the public about the importance of these less visible plant species.
- 5) Nitrogen Fertilization Strategies: Examining the effects of different nitrogen fertilization rates, timing, and forms of application on plant productivity and resilience is essential for developing effective and sustainable nitrogen fertilization strategies for semi-arid savanna biome ranches or any protected areas, based on the inclusive output on the effect on the effect of \Nitrogen fertilizer on biomass production.
- 6) Future research should focus on the following aspects:
 - Long-term Monitoring: Conducting long-term studies to capture the full range of ecological responses and adaptations to environmental stressors and management interventions is crucial for understanding the long-term impacts of these factors on plant productivity and resilience.
 - Spatial Expansion: Expanding research to encompass a wider range of sites and environmental conditions will provide a broader understanding of the generalizability of the findings and inform management strategies across diverse semi-arid savanna ecosystems.
 - Grazing Management Optimization: Investigating the effects of different grazing intensities, timing, and selectivity on plant productivity and resilience will help to optimize grazing management strategies for enhancing plant recovery from drought and promoting long-term ecosystem health.

6.5 Policy Implications

The findings of the present study have significant implications for policy decisions and management strategies aimed at conserving biodiversity, promoting plant productivity, and enhancing ecosystem resilience in semi-arid savanna ecosystems. Policy frameworks should incorporate adaptive grazing management practices, precision nitrogen fertilization techniques, and comprehensive monitoring programs to ensure sustainable land management practices. Additionally, policies should promote conservation efforts focused on protecting less common PFTs, which play a crucial role in maintaining ecosystem diversity and resilience.

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Appendices

Appendix 1 Factorial ANOVA for ANPP during versus recovery

| Source | DF | SS | MS | F | Р |
|--------------------|-----|--------|---------|-------|--------|
| SampYear | 2 | 34069 | 17034.5 | 19.92 | 0.0000 |
| Treatment | 3 | 550 | 183.4 | 0.21 | 0.8864 |
| SampYear*Treatment | 6 | 11234 | 1872.3 | 2.19 | 0.0420 |
| Error | 833 | 712265 | 855.1 | | |
| Total | 844 | | | | |

Appendix 2 Factorial ANOVA for Plant functional during drought and postdrought

| Source | DF | SS | MS | F | Р |
|------------------------|-----|--------|---------|------|--------|
| SampYear | 2 | 9602 | 4800 | 5.71 | 0.0034 |
| Treatment | 3 | 94 | 31.29 | 0.04 | 0.9904 |
| PFT | 3 | 14259 | 4752.99 | 5.65 | 0.0008 |
| SampYear*Treatment | 6 | 5099 | 849.77 | 1.01 | 0.4169 |
| SampYear*PFT | 6 | 5638 | 939.63 | 1.12 | 0.3500 |
| Treatment*PFT | 9 | 7415 | 823.88 | 0.98 | 0.4551 |
| SampYear*Treatment*PFT | 18 | 7901 | 438.95 | 0.52 | 0.9488 |
| Error | 797 | 670087 | 840.76 | | |
| Total | 844 | | | | |

Appendix 3 Factorial ANOVA for Plant functional type per sampling year per treatment.

| Source | DF | SS | MS | F | Р |
|------------------------|----|-------|---------|------|--------|
| SampYear | 3 | 10394 | 3464.55 | | |
| Treatment | 3 | 43 | 14.35 | 5.47 | 0.0010 |
| PFT | 3 | 13161 | 4387.10 | 0.02 | 0.9954 |
| SampYear*Treatment | 9 | 5503 | 611.46 | 6.92 | 0.0001 |
| Samp*PFT | 9 | 12561 | 1395.68 | 0.96 | 0.4675 |
| Treatment*PFT | 9 | 5385 | 598.33 | 2.20 | 0.0197 |
| SampYear*Treatment*PFT | 27 | 10909 | 404.03 | 0.94 | 0.4854 |

| Error | 1245 | 788936 | 633.68 | 0.64 | 0.9243 |
|-------|------|--------|--------|------|--------|
| TOTAL | 1308 | | | | |

Appendix 4 ANOVA for fertilized anpp under post-drought

| Source | DF | SS | MS | F | Р |
|------------|----|---------|---------|------|--------|
| Block | 1 | 1144.5 | 1144.51 | | |
| Fertilizer | 1 | 85.4 | 85.35 | 0.05 | 0.8199 |
| Error | 56 | 91324.6 | 1630.80 | | |
| Total | 58 | | | | |

Appendix 5 ANOVA for unfertilized plant functional type

| Source | DF | SS | MS | F | Р |
|--------|----|---------|---------|------|--------|
| Block | 1 | 1407.3 | 1407.31 | | |
| PFT | 3 | 4392.4 | 1464.13 | 0.91 | 0.4430 |
| Error | 54 | 87017.6 | 1611.44 | | |

Appendix 6 ANOVA for species composition

| Source | DF | SS | MS | F | Р |
|---------|------|--------|---------|------|--------|
| Block | 3 | 4309 | 1436.29 | | |
| Species | 29 | 62500 | 2155.16 | 3.36 | 0.0000 |
| Error | 1276 | 817688 | 640.82 | | |
| Total | 1308 | | | | |