VEGETATIVE AND REPRODUCTIVE BIOMASS ALLOCATION RESPONSES OF HERBACEOUS PLANT SPECIES TO INDUCED DROUGHT IN A SEMI – ARID HIGHLAND SAVANNA, CENTRAL NAMIBIA

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ABSTRACT

Namibia's arid conditions renders its vegetation vulnerable to changes in precipitation, affecting plant growth and biomass allocation. Recurring droughts, intensified by climate change lead to alterations in biomass allocation. Thus resulting in the reduction of medicinal products, livestock fodder, and food sources while disrupting nutrient cycles. This study investigated herbaceous drought responses in biomass allocation and the influence of environmental variables on these patterns, aiming to inform ecosystem management to conserve Namibia's biodiversity. Twenty fixed rainout shelters (4 m x 4 m) were used at Neudamm Agricultural Farm to simulate drought conditions with four treatments (0%, 20%, 40%, and 80% rainfall reduction), each replicated five times. Environmental parameters, including temperature (measured with a mercury thermometer), soil moisture content and chlorophyll content (using a SPAD-502 Plus Chlorophyll meter) were recorded before biomass harvesting. Biomass was collected from 0.5 m x 0.5 m quadrants, with aboveground biomass clipped at ground level and belowground biomass obtained through soil excavation. The Generalized Linear Models indicate that drought treatments are significant predictors of reproductive biomass allocation ($\chi^2(3) = 13.114$, $p < 0.004$), while temperature significantly influences vegetative biomass allocation ($\chi^2(1) = 17.103$, $p < 0.004$). The Friedman test results show a significant difference in chlorophyll content across drought treatments ($\chi^2 = 18.456$, $df = 1$, $p < 0.001$), with *Aptosimum lineare* and *Ocimum americanum* exhibiting the highest chlorophyll levels under treatment 60 highlighting the resilience of these species in arid savannas. These findings underscore the significant impact of drought on biomass allocation and the need for targeted interventions to mitigate its effects on plant growth and development.

Keywords: Climate change, Drought, Rainout shelters, Herbaceous plants, Namibia

LIST OF PUBLICATION(S)/CONFERENCE(S) PROCEEDINGS

1. National Students' Research Symposium (22 August 2024) (10 minutes)

   Topic: Vegetative and reproductive biomass allocation responses of herbaceous species to drought in a semi – arid highland savanna, central Namibia

   Presenter: Martha Etuna Nashini

2. Southern African Wildlife Management Association conference (09 October 2024) (5 minutes)

   Topic: Biomass Allocation of Herbaceous Species in Response to Drought

   Presenter: Martha Etuna Nashini

3. Conference of Wildlife and Tourism Management (21-22 October 2024) (15 minutes)

   Topic: Vegetative and reproductive biomass allocation responses of herbaceous species to drought in a semi – arid highland savanna

   Presenter: Martha Etuna Nashini

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LIST OF ABBREVIATIONS AND/OR ACRONYMS

AGB - Aboveground biomass

ARMS - Automatic rainfall manipulation system

BGB - Belowground biomass

CCA - Canonical Correspondence Analysis

CNKI - China National Knowledge Infrastructure

HCA - Hierarchical Cluster Analysis

IPCC - Intergovernmental Panel on Climate Change

ND - Neudamm

NPP - Net primary productivity

OPTIMASS - Options for sustainable geo-biosphere feedback management in savanna systems under regional and global change

PSF - Plant- soil feedback

R – Replicate

RepBio - Reproductive biomass

ROS - Reactive oxygen species

RS- Root to shoot ratio

SoiMoi - Soil moisture

SRL - Specific root length

SRSA - Specific root surface area

Temp - Temperature

Treat - Drought treatment

VegBio - Vegetation biomass

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DEDICATION

This thesis is lovingly dedicated to my cherished grandmother, Kuku Maria Mateus, who departed from this world on July 23, 2024, during a pivotal moment in my academic journey. Though you have left this life, your voice of unwavering encouragement and the invaluable motivation you provided continue to resonate deeply within me. Your spirit remains a guiding light in my heart. Rest in eternal peace, my dearest and beloved grandma; your love will forever be my anchor.

DECLARATION

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Martha Etuna Nashini		October 2025
Name of Student	Signature	Date

CHAPTER 1

1. INTRODUCTION

1.1 Background of study

In Namibia, the semi-arid highland savanna accounts for 5.5% of the land area (Coetzee, 1998) and it is characterized by environmental limitations such as high temperatures, erratic precipitation and frequent droughts (Gaur & Squires, 2018). These factors collectively render this region highly susceptible to shifts and variations in climate conditions. Models used by the IPCC indicate that the semi – arid highland savanna will experience increased dryness and water scarcity coupled with soil degradation and erosion which may reach an irreversible stage (El-Beltagy & Madkour, 2012). According to Sun et al. (2022), climate change is anticipated to profoundly escalate the severity and frequency of drought in semi – arid highland savanna due to their fragile ecosystems. By definition, drought is a repetitive severe weather occurrence on land, distinguished by lower-than-average rainfall and frequently accompanied by high temperatures persisting for several months to years (Dai, Zhao & Chen, 2018).

Drought has proven to be a highly destructive phenomenon in Namibia, causing significant damage to its ecosystems, impacting the economy, and playing a major role in exacerbating poverty within the country (Lombe et al, 2024). According to Liu and Zhou (2021), Namibia's arid conditions make its vegetation highly susceptible to climate change, and unusual alterations in precipitation patterns during the growing season can severely restrict vegetation growth. Eziz et al. (2017), alluded that drought serves as a significant abiotic constraint, restricting not only the growth and productivity of herbaceous plants but also affecting its biomass allocation. Biomass allocation pertains to the distribution of collective mass of organic constituents within a plant (Odum, 1953), across various components such as roots to shoots (Litton et al., 2007). The allocation of biomass patterns in plants are determined by the genotype and refined via the process of natural selection over time to modify its chances of survival (Moolman, van Rooyen & van Rooyen, 1996).

Biomass is the most feasible variable for assessing resource allocation in plants as it directly relates to their fitness and reproductive success (Eziz et al., 2017). Additionally, Kumar et al. (2011) stated that biomass allocation estimations and productivity are crucial for assessing the status and flux of biological materials in an ecosystem and for understanding ecosystem dynamics. Moreover, the distribution of plant biomass exemplifies the evolutionary survival tactics of plants across various environments, developed over extended periods in response to environmental changes and stresses (Wang et al., 2024).

Manipulative experiments have served as an alternative way of investigating the relationship of inter annual variation of productivity and precipitation instead of waiting for completion of long term data set. Field water manipulations, as opposed to greenhouse manipulations are more ideal for addressing issues relating to changes in water availability due to their accuracy in measuring natural conditions (Yahdjian & Sala, 2002). Additionally, they provide valuable insights into the potential impacts of different climate change scenarios on ecosystems (Yahdjian & Sala, 2002). Following the latter statement, Kreyling et al. (2017), asserted that field water manipulations have proven to be powerful tools for the causal understanding of ecological processes in the face of climate change.

Primarily, rainout shelters that erect over an intact population of vegetation are utilized to exclude ambient precipitation from a predefined experimental area (Hoover, Wilcox & Young, 2018).

Rainout shelters are effective experimental tools that are designed to exclude natural precipitation which makes them ideal for most drought simulation models. Rainout shelters have been instrumental in enabling a wide range of studies, including evaluations of crop species' drought resistance, investigations into water relations of rangeland and desert shrubs, examinations of the relationship between water and nitrogen availability, and assessments of how rainfall chemistry impacts the growth and nutrient cycling of plantations (Yahdjian & Sala, 2002). Additionally, rainout shelters offer flexibility in experimental design and site selection, as well as the opportunity to carry out long-term experimental manipulations (Fay et al., 2000). Rainout shelters range from small, fixed structures intended to exclude rainfall from the root zones of a single plant to moveable, building sized structures (Fay et al., 2000). Despite the variations in size, all shelters adhere to some basic design criteria, with the primary objective being effective exclusion of rainfall. Additionally, the shelters should minimize changes to microclimate conditions aside from rainfall exclusion and endure unfavorable weather conditions (Foale et al*.,* 1986).

Comprehending how changing precipitation treatments impacts herbaceous plants biomass allocation is vital for landscape management as it entails species adaptations and distributions. Although essential for plant survival, the precise impact of drought stress on biomass allocation, particularly concerning reproductive organs, is not fully understood, especially in herbaceous species.

1.2 Statement of the problem

Namibia has faced recurring droughts spanning more than seven years, hitting in 1992/1993, 1995/1996, 2012/2013, 2013/2014, 2015/2016, and 2018/2019 (IFCR, 2022). The drought events have resulted in higher livestock and wildlife mortality rates due to reduced fodder and water availability. Additionally, shortages of plant-derived food and medicinal resources, along with a decrease in other ecosystem benefits, have negatively impacted the livelihoods of local communities. With drought becoming more persistent, herbaceous plants may be expected to prioritize survival over vegetative growth. Thus potentially reducing the benefits acquired from them such as medical products, fodder for livestock and edible food sources for human consumption and impact the nutrient cycling (Trimble, 2020). Therefore, it is vital to investigate biomass allocation patterns of herbaceous plants as they could be changing due to the shifting rainfall patterns.

1.3 Research objectives

The main objective was to assess vegetative and reproductive biomass allocation of herbaceous species under different drought treatments in a semi – arid highland savanna, Neudamm farm. The specific objectives of this study were to:

a) Compare above-ground and below-ground biomass allocation of herbaceous plants across drought treatments at Neudamm farm.
b) Compare vegetative and reproductive biomass allocation of herbaceous plants across drought treatments at Neudamm farm.
c) Determine the correlation between soil moisture content and biomass allocation across drought treatments at Neudamm farm.

d) Determine the effect of soil moisture content, species and drought treatments on vegetative biomass allocation and reproductive biomass allocation.

e) Determine the effect of shading on photosynthetic capacity of specific herbaceous species across drought treatments at Neudamm farm.

f) Determine the effect of drought treatment on herbaceous plant cover at Neudamm farm.

g) Determine the correlation between biomass allocation and herbaceous plant cover under drought treatments.

h) Compare species composition of herbaceous species across drought treatments.

1.4 Research hypotheses

a) Herbaceous species will allocate more biomass belowground under dry conditions to maximize their chances of acquiring water and nutrients.

b) As drought stress increases, more biomass will be allocated to vegetative structures than reproductive structures to conserve resources (i.e. water and nutrient).

c) An increase in soil moisture levels will promote greater vegetative and reproductive biomass allocation as adequate soil moisture enhances plant physiological processes, such as photosynthesis and nutrient uptake.

d) Increased drought stress will lead to a reduction in overall biomass allocation, due to declining soil moisture content and the prevalence of non-drought-tolerant species.

e) Photosynthesis capacity will decline with increase in drought stress due to the possible loss of light energy that may be reflected or absorbed by the 100-micron clear plastic sheet used for rain shelters.

f) Herbaceous plant cover is expected to decline with increase in drought stress as aboveground investment will be reduced as a survival strategy.

g) As drought stress increases, herbaceous plant cover is expected to decline as a survival strategy under unfavorable conditions, leading to a reduction in overall biomass.

h) Species composition of herbaceous plants will vary significantly under drought treatments due to species-specific traits that influence their adaptability and survival strategies.

1.5 Significance of the study

The study helps us understand how herbaceous species in a semi-arid savanna ecosystem might respond to drought, with a focus on biomass allocation. Understanding how herbaceous plant species respond to drought is essential because it provides insights into the resilience and adaptability of these plants, which is crucial for effective ecosystem management and conservation efforts tailored to the changing climate conditions (Liu & Zhou, 2021). Since herbaceous plants play essential roles in providing ecosystem services such as soil stabilization and carbon sequestration, understanding how drought affects their vegetative and reproductive biomass allocation can provide valuable information on the resilience of these ecosystem services to changing environmental conditions. This study further assists in anticipating changes in forage availability and inform sustainable land use practices to ensure food security and livelihood sustainability for local communities. Findings can also be used to guide future research into allocation patterns, especially in a context of environmental change as few exist in arid ecosystems.

CHAPTER 2

2. LITERATURE REVIEW

Comparison of above- and below-ground biomass allocation in herbaceous plants under drought conditions

Drought typically induces predominantly neutral or negative responses in herbaceous plants in terms of growth and biomass (Liu & Xu, 2021). The differential distribution of resources across various structures and functions in plants is crucial for their ability to adapt and respond effectively to environmental changes. Moreover, biomass allocation holds significance as it can impact various factors such as livestock nutrition, soil integrity, and carbon storage (Liu & Xu, 2021). To better comprehend biomass allocation in terms of aboveground and belowground allocations, the optimal partitioning theory and the isometric partitioning theory have been used. According to the optimal partitioning theory, it stipulates that plants allocate more biomass to organs that acquires the most resources (Bloom et al., 1985). Hence, it is anticipated that plants will allocate a greater proportion of biomass to belowground structures during dry conditions, while allocating more biomass aboveground when experiencing wet conditions (Villar et al., 1998 cited in Liu & Xu, 2021). In support of the latter, leaf biomass is known to correlate with the 3/4 power of both stem and root biomass allometrically, whereas root biomass scales isometrically with stem biomass (Dolezal et al. 2021). On the other hand, the isometric partitioning theory proposes that both aboveground and belowground biomass exhibit a proportional relationship, suggesting that there may not be a clear trade-off between these two biomass components (Wang et al., 2014). However, conflicting findings have emerged, with some studies supporting isometric partitioning and others refuting it which calls for additional research to provide greater clarity on this theory (Liu & Xu, 2021).

The root to shoot ratio (RS) serves as a useful metric for characterizing the allocation between aboveground biomass (AGB) and belowground biomass (BGB) (Wang et al, 2014). Consequently, it functions as a convenient tool for estimating BGB through the relatively simple measurement of AGB under drought stress. A study conducted in Inner Mongolia, Northern China investigating the responses to altered precipitation and drought treatments of morphological traits and dry matter content of annual herbaceous plants in growing seasons, alluded that under severe drought, the root to shoot ratio varied as the root growth was increased to more efficiently exploit soil water resources (Sun et al., 2022). Moreover, the annual herbaceous plants increased their morphological traits such as root surface area, number of second-level stem branches and leaf number to better resist severe drought stress during ongoing climate change (Sun et al., 2022). Another study focusing on the contrasting responses to drought stress in herbaceous perennial legumes, affirmed that morphological adaptations to drought stress were observed in some species, such as leaf hairs and leaf curling, which reduce transpiration rates by increasing the thickness of the laminar layer over the leaf (Pang et al. (2011). These findings are in agreement with conclusions that plants tend to increase their root system investments at the expense of shoot mass with drought (Eziz et al, 2017). Eziz et al. (2017), further alluded that under drought, herbaceous plants invested less to the stem and leaf to reduce the water loss to minimum level hence the stem and leaf mass fractions reduce significantly. This is also consistent with research on biomass allocation to leaves, stems and roots, which found higher root mass fraction and lower leaf and stem mass fractions under water scare conditions (Poorter et al. 2012).

The allocation from leaf to roots is crucial as it impacts the plants assimilation capacity, growth rate and net primary production. Previous research suggests a significant positive relationship between aboveground biomass and net primary productivity (NPP), with biomass being the main factor driving NPP. It is proposed that when NPP rises in a given area, it indicates vegetation in that area is accumulating more biomass through increased aboveground growth, leading to reduced belowground biomass production (Wang et al., 2024). Moreover, aboveground and belowground biomass allocation patterns also provide essential information for linking the aboveground productivity and belowground carbon sequestration (Sun et al., 2022). Most of the existing studies have only assessed aboveground biomass, disregarding belowground biomass since it is more difficult to quantify, especially in the field (Ma et al., 2008). Hence, comprehensive knowledge of changes in plant allocation patterns in response to drought is generally lacking and allocation strategies merit further investigation.

Comparison of vegetative and reproductive biomass allocation in herbaceous plants under drought conditions

The allocation of resources among various structures or functions plays a crucial role in shaping the overall fitness and reproductive success of plants within specific environments or communities (Eziz et al. 2017). Reproductive biomass is measured as the ratio between seed and total biomass (Ploschuk, Slafer & Ravetta, 2005) whilst vegetative biomass takes into account the shoot excluding the reproductive organs. A meta-analysis study which synthesized 164 published studies from Web of Science, Google Scholar, Scopus, and

China National Knowledge Infrastructure (CNKI) aimed at investigating patterns of plant biomass allocation under drought stress revealed that herbaceous plants tend to decrease investment in reproductive structures under drought conditions which is attributed to decreased photosynthesis and alterations in phenology (Eziz et al. 2017). Drought stress also affects flower maturation as the number of mature flowers on the plant stems can significantly be reduced with increase in drought stress (Su et al. 2013). The reduction of adequate water availability impacts the expansion/elongation of floral organs (Su et al., 2013). These studies have illustrated that under extreme drought stress, herbaceous plants will invest more into vegetative biomass at the expense of reproductive biomass.

Biomass allocation to vegetative and reproductive organs may differ for annual and perennial plant species. A study by Eziz et al. (2017), found that root biomass of perennial herbs is less sensitive to drought stress compared to annuals which have a relatively short life span. They further argued that annual herbaceous plants tend to prioritize current reproduction and growth over storage and defense mechanisms such as roots and stems while perennials which are more resource-conserving, invest more in defense and storage. Interestingly, during drought, vegetative structures of perennial herbs shows a mild increase while those of annuals decrease significantly, possibly due to differences in plant size during development (Eziz et al., 2017). In accordance with their findings, Li et al. (2021) asserted that perennial species tend to adopt the “fight” strategy under drought conditions as they allocate more resources to survival mechanisms aimed at vegetative growth or defense at the expense of sexual reproduction while annuals choose the “flight” strategy with the aim of investing in potential offspring that might encounter better conditions than the parent itself. Since perennials grow and reproduce over several season, increased survival is likely to increase lifetime reproductive output compared to increased reproduction in any one year (Li et al., 2021). In contrast, findings by Staley, Mortimer and Morecroft, (2008), revealed that annual and perennial species reacted similarly to drought stress as both prioritized vegetative growth over reproductive under water stress.

Influence of soil moisture content on herbaceous biomass allocation under drought conditions

Soil moisture content which is known as the amount of water contained in a particular soil volume (Or, Wraith & Warrick, 2002) plays a vital role in biomass allocation patterns of herbaceous species. Soil moisture in frequently occurring drought events largely constrains vegetation growth as well as biomass allocation in semiarid and arid savannahs (Yang et al., 2011). A study conducted in China, based on evaluating the effects of soil water conditions on biomass allocation of plants using rainout shelters illustrated that, limited soil water content decreases the total biomass production, particularly of grasses which might be ascribed to inhibited photosynthetic performance under soil water deficit (Xu et al., 2022). In line with their findings, a study conducted at Naiman, Mongolia on biomass allocation to vegetative and reproductive organs of *Chenopodium acuminatum* under water stress using rainout shelters concluded that, at low soil water conditions the plants allocated more biomass to vegetative rather than to reproductive organs as a survival tactic (Huang et al., 2013).

Drought has also been known to modify plant- soil feedback (PSF) which occurs when a plant species changes the microbial, chemical, or physical properties of the soil it is grown in, in a way that it affects the performance of subsequent generations of plants either positively or negatively (Fry et al., 2018). Negative plant-soil feedback can arise from resource depletion or the excretion of autotoxic compounds (Bennett & Klironomos, 2019). Under drought stress, the PSF can be altered through changes in soil moisture content, root exudation patterns in response to water availability and reduction in plant – mutualistic organisms (Wilschut & van Kleunen, 2021). The latter is evidently proven in a study by Wilschut and van Kleunen (2021) which demonstrated that drought significantly influences plant-soil feedback effects on biomass allocation. Their findings indicate that variations in soil moisture can impact how plants allocate biomass, as all species examined exhibited reduced growth and reproductive success in response to declining soil moisture levels (Wilschut & van Kleunen, 2021). Inconsistent with their findings, Fry et al. (2018) revealed that drought can neutralize the effects of PSF on the growth of forb plants. This further supports the notion that soil moisture levels can significantly alter plant-soil feedback outcomes.

In contrast to previous findings, some studies have shown that vegetation types and structure also have significant impacts on soil moisture dynamics therefore limiting the effects of drought on soil water content. Vivoni et al. (2008) stated that vegetation can mediate the soil moisture response to precipitation and change the spatial distribution of soil moisture, while Yang et al. (2012) found that plant growth conditions can change the spatial pattern of shallow and deep soil moisture in semi-arid regions. To add on, vegetation coverage and grass stem density play pivotal roles in regulating soil water loss and run off by impacting the microchannel and runoff characteristics (Yang et al., 2012). A study conducted in semi-arid steppes on the Loess Plateau of China focusing on interactions of soil water content heterogeneity and species diversity patterns revealed that herbaceous vegetation with larger aerial coverage and their litter protects the soil against the erosive forces of rainfall and therefore increases soil water uptake (Wu et al., 2014). The study suggested that there is a positive interaction effect between herbaceous plant coverage and soil water content (Wu et al., 2014).

Impacts of shading on photosynthetic capacity of herbaceous plants under drought conditions

Drought is the most severe environmental factor that inhibits photosynthesis and limits plant productivity in both natural and agricultural systems. In semi-arid and arid regions, drought is usually accompanied by light and high temperature stress which constraints plant growth (Athar & Ashraf, 2005). Plant growth is decreased through reduction of the photosynthetically active leaf area, lowering of water potential of the growing plants, decrease in stomatal conductance and alteration in chlorophyll fluorescence (Dubey, 1997 cited in Athar & Ashraf, 2005). In addition, drought stress can also lead to the suppression of photosynthetic genes and disruption of transcripts encoding of some glycolysis and pentose phosphate pathway enzymes (Siddique, 2016). Moreover, under drought stress, photosynthetic activity is inhibited in plant tissues as a result of the imbalance between light capture and utilization (Luo et al., 2023). Decreased photosynthetic capacity due to drought stress not only hampers the plant growth but also is directly/indirectly associated with the reduction of yield and quality in medicinal herbaceous plants (Luo et al., 2023).

The root/shoot ratio in plants serves as an alternative method to reflect the differential investment of photosynthesis between the aboveground and belowground organs (Luo et al., 2023). Luo et al. (2023) further alluded that an increased root/shoot ratio suggests more investment of photosynthesis into belowground parts. Additionally, several studies have shown that chlorophyll concentration can also be an indicator for the evaluation of photosynthetic under drought stress experiments. Reduction in chlorophyll concentration has been considered a nonstomatal limiting factor and a kind of protection mechanism for photosynthetic structures under drought stress (Bhusal et al., 2020a). In support of the latter, a study focused on morphology, photosynthetic physiology and biochemistry of nine herbaceous plants under water stress concluded that, decline in chlorophyll content resulted in low photosynthetic activities under drought stress as water stress induced the production of reactive oxygen species (ROS), such as O2 and H2O2, which led to lipid peroxidation and consequently chlorophyll and carotenoid destruction (Luo et al., 2023). Their findings are in agreement with those of Chen et al. (2016) who found that the chlorophyll a/b ratio decreased under drought stress, implying a more severe effect on the photosynthetic performance as cellular homeostasis was disrupted and electrons were transferred to molecular O2 to form ROS, which ultimately caused photo inhibition and oxidative damage. Consistent with the findings of (Luo et al., 2023, Chen et al., 2016), a study that investigated the effect of drought on photosynthesis of *Atractylodes lancea,* alluded that photosynthesis was inhibited due to stomata closure which induced reduced CO2 supply and further caused metabolic impairment (Zhang et al., 2021). It is vital to note that the sensitivity to environmental changes such as drought in photosynthesis varies among plant species (Wang et al., 2019). As some species possess the ability to recover quicker than others from drought events and some might not show significant changes.

Influence of temperature on biomass allocation under drought conditions

Temperature is another environmental factor that can also affect plant performance in terms of biomass allocation. A study that assessed the combined effects of warming and drought on plant biomass, found that warming (increase in temperature) did not strengthen or weaken effects of increased precipitation or drought on herbaceous plant biomass (Wilschut et al., 2022). The study further suggests that biotic contexts, such as plant growth form and plant community type are to account for biomass responses to combined effects of warming and drought (Wilschut et al., 2022). In contrast, a study focused on the interactive effects of elevated temperature and drought on plant carbon metabolism concluded that the effect of temperature and drought on plant biomass displayed a negative interaction with temperature worsening the drought impacts (Wang & Wang, 2023). It also alluded that perennial herbs exhibited a stronger amplifying effect of temperature on plant biomass in response to drought than did annual herbs (Wang & Wang, 2023). Consistent with their finding, a study which assessed the negative interaction effect of heat and drought stress on species distribution discovered that an increase in temperature and lower precipitation/watering had a negative effect on plant survival, and combined stress had a worse than additive effect on survival (Schepers, Heblack & Willi, 2024). It further revealed that the size of herbaceous plants reduced and the plants hardly flowered under heat and drought (Schepers, Heblack & Willi, 2024). Hamann, Kesselring and Stöcklin (2018) affirmed that low temperatures decrease aboveground biomass as well as constrains plant growth. Additionally, low temperatures limit intake of water and nutrients from the root system which reduces tissue nutrient concentrations and thus decreases root growth (Kul et al., 2020). However, little is known about how temperature and precipitation extremes affect plant performance belowground, and in particular, which factor may underlie the magnitude of such combined effects (Wilschut et al., 2022).

CHAPTER 3

3. RESEARCH METHODS

3.1 Study site

3.1.1 Location and Extent

The study was conducted at the Neudamm Agricultural Farm, located at the University of Namibia, Neudamm Campus and situated between 22°30.105'' S and 017°20.824" E central Namibia, Khomas Region and at altitude 1856 m above the sea level (Kahumba et al., 2022). The farm covers 10 187 ha of land and is divided into 9 blocks (A-J) with 197 smaller grazing camps (Kahumba, 2010). Neudamm was selected because it is one of the few sites known to have fixed rainout shelters in Namibia.

3.1.2 Climate

The climatic conditions of the study area are an arid to semi-arid highland savannah. The average annual rainfall ranges from 300mm-360 mm (Kahumba et al., 2022) with 80% of the annual rainfall occurring in the summer months between January and March.

3.1.3 Physical features, geology and soils

The soil type in the study area is dominated by homogenous Lithic Leptosols and Eutric Regosols, which are generally shallow and contain very little organic matter, which has been attributed to low organic litter input and rapid mineralization (Shigwedha, 2020). The farm soils have a clay content of less than (5%), and thus have a very low water holding capacity (Kapu, 2012). Additionally, the soil is covered with quarzitic pebbles which improves soil moisture and are also skeletic on the slopes, where they can turn into blockfields and bare bedrock (Kapu, 2012)

3.1.4 Flora and fauna

The vegetation type in this area is categorized as semi - arid highland savanna and occupies approximately 45 000 km^2 of Namibia's land area (Shilume, 2020). The Highland savanna is dominated by *Senegalia mellifera* (Vahl) Seigler & Ebinger and also characterized by shrubs and low trees. The undisturbed rangelands consist of climax grasses such as *Anthephora pubescens* (Steud.) Nees, *Schmidtia pappophoroides* Steud. ex J.A. Schmidt, *Brachiaria nigropedata* Munro ex Ficalho & Hiern) Stapf, *Heteropogon contortus* P.Beauv. ex Roem. & Schult and *Digitaria eriantha* Steud (Kahumba et al., 2022). In terms of fauna, the Farm is housing large and small livestock. The large stock consists of Sanga, Simmentaler and horses (Arabierx-Boer horse breed). The small stock has different breeds of sheep and goats (Boer goat, Swakara, Dorper and Damara sheep). In addition, there are wild animals in the Farm such as kudus, oryx, red hartebeests, warthogs, waterbucks and baboons (Shilume, 2020).

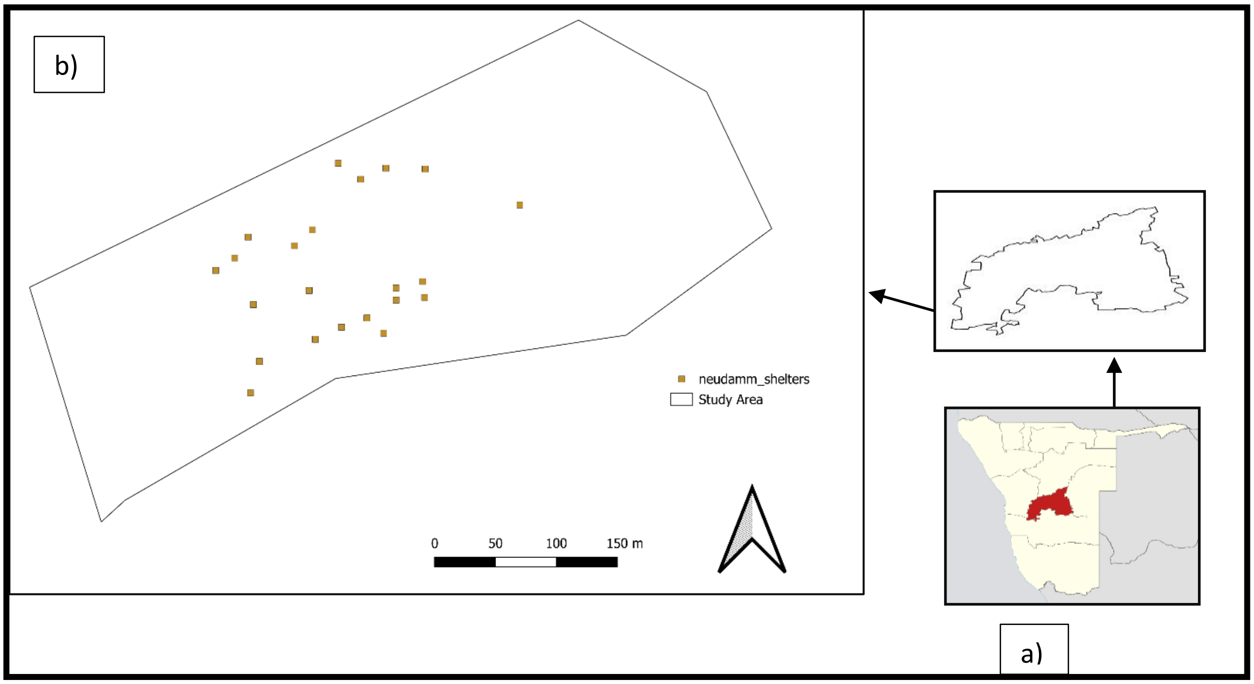


Figure 1. Map of study area displaying the specific locations of the rainout shelters within the study area (b) at the Neudamm Field Site in Khomas region (a) Namibia. The rainout shelters were data was collected from are represented by the brown squares found in the image on the left.

3.2 Research design

The study employed a Randomized Block Design because it grouped experimental units (rainout shelter plots) into blocks to control for known sources of variation, such as environmental factors (i.e. temperature and rainfall). By randomly assigning treatments (different levels of rainfall exclusion) within these blocks, the design minimizes the impact of nuisance variables, thereby enhancing the accuracy and reliability of the results. This approach allows for a more precise comparison of treatment effects by reducing variability within each block compared to the entire sample.

3.2.1 Rainout shelter design

Rainout shelters are experimental structures equipped with transparent roofing material, designed to intercept known amounts of rainfall for ecological research on plant-climate interactions within an ecosystem (Hoover, Wilcox & Young, 2018). These structures are designed to minimize disruption to the microclimate, thus enabling photosynthesis to proceed with minimal disturbance (Fay et al., 2000; Gherardi & Sala, 2013). The shelters utilized in this study follow the design of the automatic rainfall manipulation system (ARMS) outlined by Gherardi and Sala (2013). However, the shelters in this study designed to simulate drought conditions, lacking the additional components for collecting and supplementing rainfall as described in Gherardi and Sala (2013). Furthermore, unlike the shelters in Gherardi and Sala (2013), the plots were not lined with waterproof lining around the edges to regulate control surface and sub-surface water movement.

The fixed location rainout shelters measuring 4 m x 4 m in ground dimensions and covering an area of 16 m^2 were used for this study. The roof of the shelters is partitioned into twenty, 20 cm wide spaces each of which were each lined with 2 rows of 4 mm wash line rope and an additional rope for where the covering could be placed, extending from the tall end to the short end of the outer frame. The 20 cm wide roof covers or shingles, made from a double layer of 100-micron clear plastic sheet were mounted to the outer wash line ropes using plastic cable ties, on either side, carefully placing the middle, low-lying rope on top and therefore creating the trough shape necessary to facilitate rainfall exclusion from the plot.

3.2.2 Rainfall exclusion treatments

The shelters in this experiment simulated four drought treatments by excluding 0% (the control), 20% (shelter only receiving 80% rainfall), 40% (receiving 60% rainfall) and 60% (receiving 40% rainfall) of the rainfall from the plots during the rainy season. These stress regimes were selected due to their provision of a clear gradation of stress levels: 0 representing optimal (control) conditions, 20 indicating mild stress, 40 denoting moderate stress, and 60 reflecting severe stress. This structured approach enhances the interpretability of experimental outcomes, as it aligns with methodologies utilized in existing literature, thereby facilitating comparative analyses and broader inferences regarding the ecological impacts of drought (Zhang et al., 2023). Furthermore, this regime is inclusive of drought predictions pertinent to dryland ecosystems (Maisnam et al., 2023).

The four drought treatments were applied to five replicate plots, totaling 20 rainout shelter plots. Since each shelter measures 4 m x 4 m, one 20 cm wide plastic shingle intercepted 5% of incoming rainfall. Accordingly, the 20%, 40% and 60% were covered with four, eight and twelve plastic shingles, respectively while the 0% drought plots were uncovered (Figure 2). The shingles were arranged at as equal intervals as possible to intercept these rainfall proportions. Rainfall data were sourced and provided by the Neudamm Campus Management office since they maintain daily rainfall records at their weather station. The total rainfall for the season was 170.5 mm. During the experiment period (March – April 2024), 115 mm of rainfall was recorded, which represents 67.4% of the total seasonal rainfall (as shown in Figure 3).

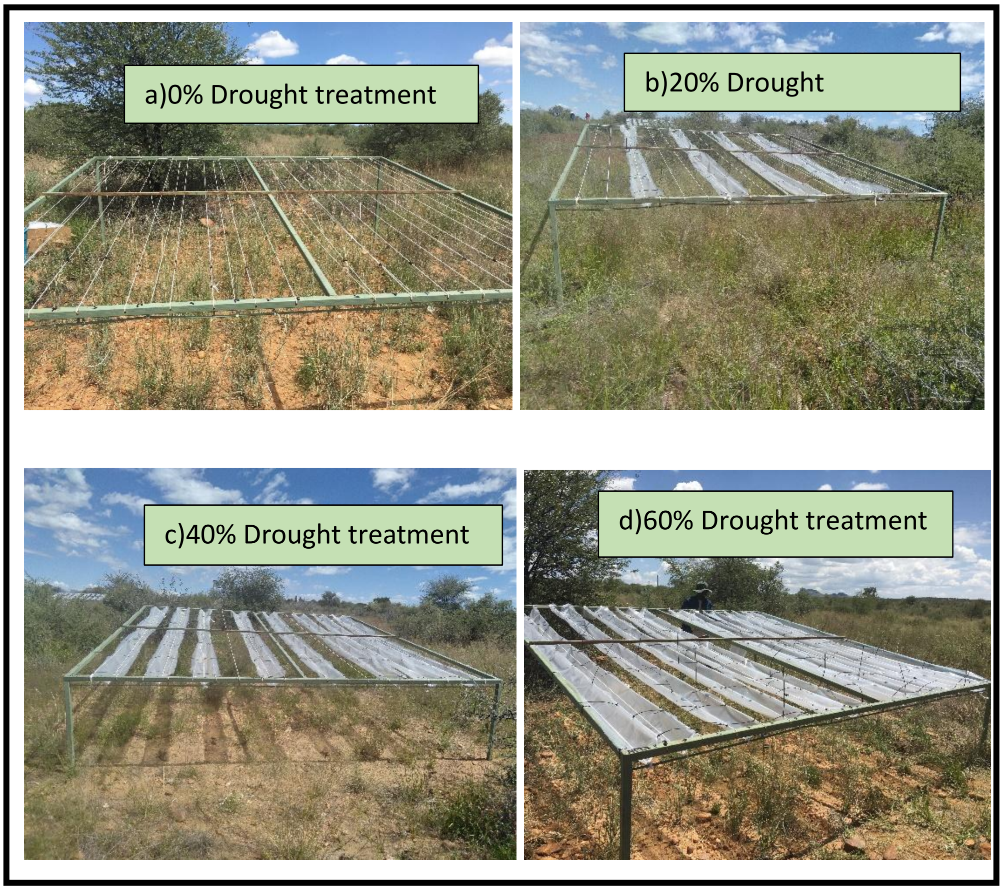


Figure 2. Design of the rainfall exclusion treatments.

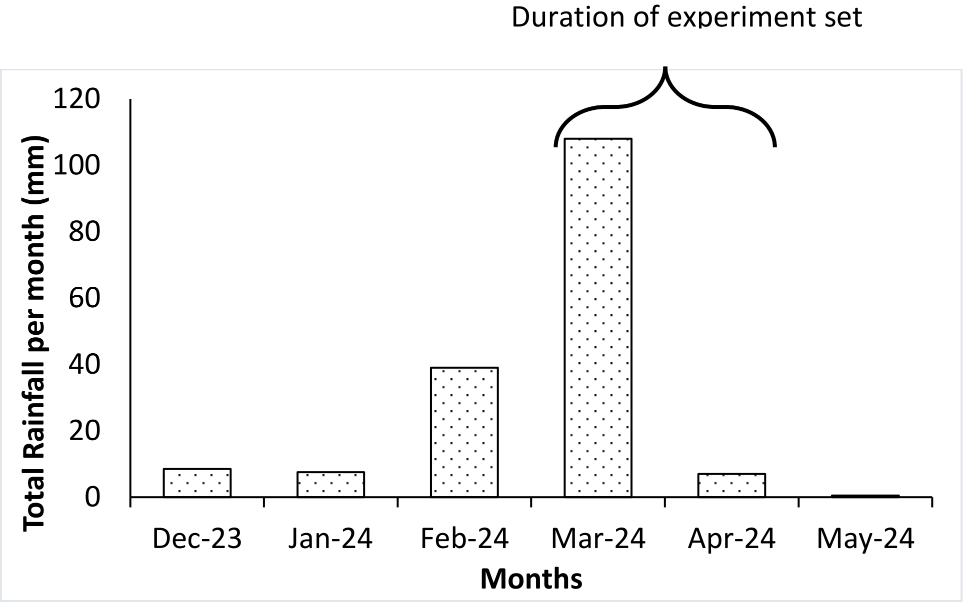


Figure 3. Total rainfall per month over the rainy season at Neudamm agricultural farm.

The study focused on herbaceous plant species with the main emphasis to examine *Aptosimum lineare* Marloth & Engl*, Aristida congesta* Roem. & Schult*, Chascanum pinnatifidum* (L.f.) E.Mey*, Chloris virgata* Sw.*, Eragrostis rotifer* Rendle *, Melinus repens* Willd.*, Ocimum americanum* L and *Urochloa brachyura* Hack that were observed during a reconnaissance trip to the field site. *Aptosimum lineare* is a low-growing perennial herb traditionally used to address gynecological issues such as menstrual disorders and to enhance female fertility. It also serves as fodder for livestock (Mongalo & Makhafola, 2018). *Aristida congesta* is a pioneer, perennial tufted grass found in disturbed areas like road reserves, abandoned cultivated lands, and overgrazed veld. It is an indicator of veld disturbance and has generally poor forage value (Van Staden & Van de Haar, 2012; Dingaan & Du Preez, 2013; Munyebvu-Chambara et al., n.d). *Chascanum pinnatifidum* is a medicinal perennial herb, with leaves used to treat muscle aches (Du

Preez, 2012). *Choris virgata* is a C4 annual grass, known for its invasiveness in bare areas and degraded or disturbed native vegetation. Despite this, it is useful for revegetation, fodder, and forage (Ngo et al., 2014; Rojas-Sandoval, 2016). *Eragrostis rotifer* and *Melinis repens* are perennial grasses valuable for livestock; both are grazed by cattle and goats and are used as thatching grass, with *Melinis repens* additionally employed for roughly woven baskets (Klaassen & Craven, 2003). *Ocimum americanum* is an aromatic herb used medicinally to treat microbial-related diseases and constipation (Luanda et al., 2023). *Urochloa brachyura* is an annual grass that serves as fodder for cattle and goats (Klaassen & Craven, 2003).

3.3 Data Collection

3.3.1 Biomass harvesting and measurements

In this study a 0.5 m x 0.5 m quadrant was used for belowground and aboveground biomass harvesting. The quadrant was randomly thrown under the rainout shelter and all the herbaceous vegetation that fell within the quadrat was harvested. Prior to the harvesting, all plant species that fell within the quadrant were identified to species level to ensure that only herbaceous plants were present. For aboveground biomass assessment, herbaceous vegetation was clipped off at ground level (representing maximum standing biomass) using secateurs. The harvested biomass was then collected and placed in brown paper bags which contained labels. The paper bags were transported to the laboratory. In the laboratory, aboveground biomass material was placed in a Scientific series 9000 oven and were left to dry for 19 hours at 50°C. After oven drying aboveground biomass material was weighed using an Adam (Milton Keynes, UK) analytical scale balance. Firstly, the whole shoot was weighed, then the inflorescences of grasses and flowers and fruits of forbs were separated from the entire plant and weighted to represent reproductive output. The stem and leaves were then weighed separately to yield the vegetative data.

Belowground biomass was obtained through the excavation method. Belowground biomass material was obtained in the same plot (i.e. 0.5 x 0.5 m metal quadrant) in which the aboveground biomass material was clipped. The soil was then excavated using a shovel to a depth of 10 cm. After excavation, the soil was then placed on the tarp where roots and other belowground organs such as corms, tubes were extracted manually with the help of sieves. The aboveground biomass was then placed in paper bags and transported to the laboratory for further analysis. In the laboratory, the roots were carefully removed from the paper bags and placed in labeled glass beakers that contained water. This was done to separate the mineral soil from root biomass and organic matter (Franks & Goings, 1998). The roots were left to soak for 2 hours in the laboratory before they were removed from the beakers. Tissue paper was used to dry the roots before being placed back into the paper bags. The roots were then oven dried for 68 hours at 50°C using a Scientific series 9000 oven. Weighing was done using an Adam (Milton Keynes, UK) analytical scale balance.

3.3.2 Chlorophyll content analysis

The amount of chlorophyll present in the plant leaves can serve as an indicator of the overall condition of the plant itself. In this study, a Chlorophyll meter SPAD-502 Plus was used to assess the chlorophyll content in some herbaceous species found under the shelters. The Chlorophyll meter SPAD -502 can measure an area of 2mm x 3mm, allowing small leaves to be measured and samples that are up to 1.2mm thick (Shibaeva et al., 2020). Before taking the readings, the instrument was calibrated by turning the power to

ON and with no sample in the sample slot, press on the finger rest to close the measuring head. A beep sound should than be head and the display should show N=0. After calibration, the sample to be measured which is the leaf was inserted into the sample slot of the measuring head. The leaf was ensured to be clean and free of dust or water. The sample was ensured to completely cover the receiving window. To take the measurement, the measuring head should be closed and a beep sound should be head. The measured values will than appear on the display. The measured values were recorded on a data sheet.

3.3.3Temperature measurements

Temperature readings were obtained under each rainout shelter using a mercury thermometer. The recorder entered the shelters and measured the temperature at the center of each rainout shelter. These readings were then documented on a data sheet. To ensure accuracy, the thermometer was stabilized by holding it by the end and shaking it until the reading reached 0°C.

3.3.4 Species composition and herbaceous cover estimates (%)

All herbaceous species that fell under the rainout shelters were identified to species level. For those that could not be identified in the field, samples were collected and pressed. The identity of the plant species was verified using taxonomic descriptions, taxonomic keys, identification guides, herbarium specimens and the help of Plant Taxonomy and Systematics Expertise at the University of Namibia. The plant percentage cover was assessed by treating the entire rainout shelter as a single plot and estimating cover for each individual herbaceous species. Initially, the cover estimates were recorded as individual values for each species and subsequently categorized into classes (i.e. <5, 5.1 -10, 10.1-20, 20>) for analysis.

3.3.5 Soil sampling for soil moisture content assessment

For soil sample collections, a small hole was dug close to the 0.5 X 0.5 m hole from which biomass was harvested. The hole was measured to be +/- 10 cm deep. Soil was then collected using a spade around the hole, making sure to scrape soil from the entire 10 cm profile. The soil samples were then placed in zip loc bags and transported to the University of Namibia, Windhoek campus laboratory for soil moisture analysis. Once in the laboratory, the study followed the gravimetric method of soil moisture determination (Brandelik & Hübner, 1996). The soil samples were firstly sieved to remove stones and debris using a sieve. Then the wet weight was weighed using an Adam (Milton Keynes, UK) analytical scale balance. The soil samples were then transported into the Scientific series 9000 oven where they were oven dried for 16 hours at 105°C. The dry weight was then weighed and soil moisture content was obtained by using this formula:

$$Soil\ moisture\ Percentage\ (\%) = \left[\frac{Wet\ Soil\ Weight - Dry\ Soil\ Weight}{Dry\ Soil\ Weight}\right] * 100$$

(Manchikanti, 2007).

3.4 Data analysis

The analysis for the first six objectives was conducted using the Statistical Package for the Social Sciences (IBM, Version 24.0). The Shapiro-Wilk test was conducted to assess the normality of the data. The results indicated that the data for objective (a), (b) and (c) were not normally distributed ($p < 0.001$) and consequently, non-parametric statistical tests were considered appropriate for further analysis. For objective a), which compared above-ground and below-ground biomass allocation, and objective b), which compared vegetative and reproductive biomass allocation across drought treatments, a Kruskal-Wallis H test was utilized. Objective c) involved analyzing the correlation between soil moisture content and biomass allocation across drought treatments using Spearman's rank correlation. To determine the effects of soil moisture content, species, and drought treatments on vegetative and reproductive biomass allocation (objective d), Generalized Linear Models with Gamma distribution were computed. For objective e), the effect of shading on the photosynthetic capacity of specific herbaceous species across drought treatments was analyzed using a Friedman test. Objective f) assessed the correlation of drought treatment on herbaceous plant cover using Fisher’s exact test. Spearman's rank correlation was once again used to determine the g) correlation between soil moisture content and biomass allocation across drought treatments. Finally, for objective h), a Hierarchical Cluster Analysis (HCA) was performed in Primer version 5.2 to compare the species composition of herbaceous species across drought treatments, while Canonical Correspondence Analysis was conducted using Canoco 5 software to visualize how various environmental conditions impact species composition.

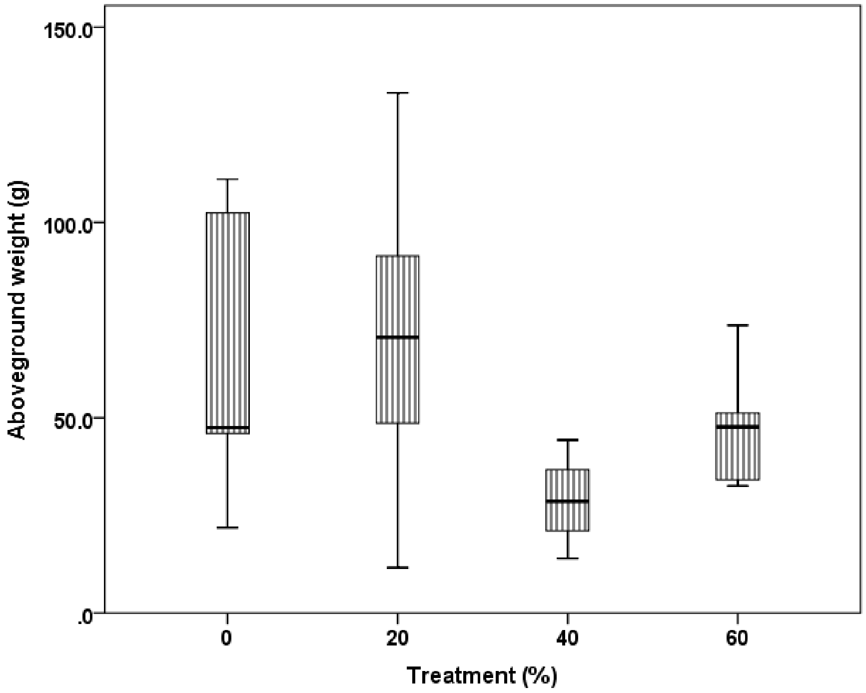
CHAPTER 4

4. RESULTS

4.1 Comparison of above-ground and below-ground biomass allocation across drought treatments

The Kruskal - Wallis H test revealed that there was no statistical significant difference between belowground and aboveground biomass allocation across the drought treatments (H = 1.740, df = 3, p > 0.628). The different levels of drought treatment (0%, 20%, 40%, 60%) do not appear to affect belowground and aboveground biomass allocation significantly (Figure 4). Across the four drought levels (0%, 20%, 40%, 60% rainfall exclusion), the allocation patterns remained relatively consistent, with slight variations but no clear trend indicating an effect of increasing drought severity.

a)



b)

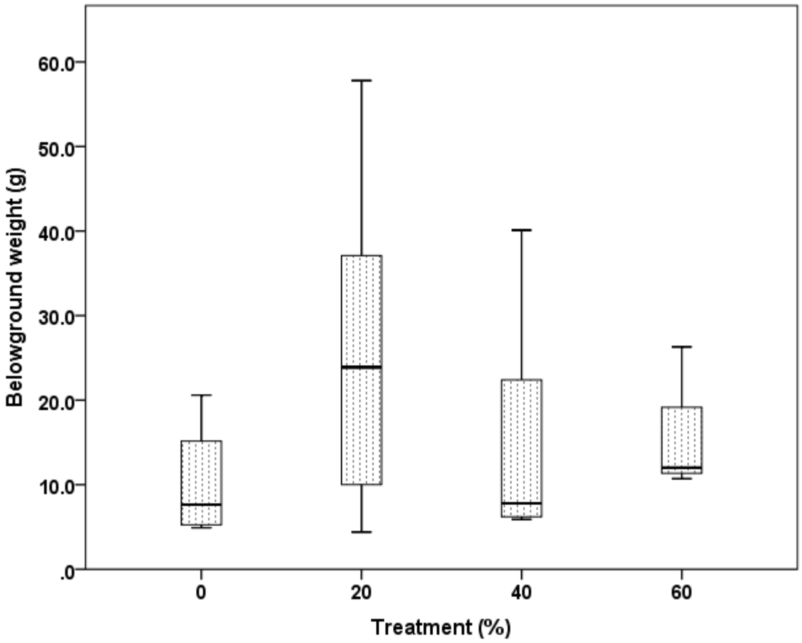
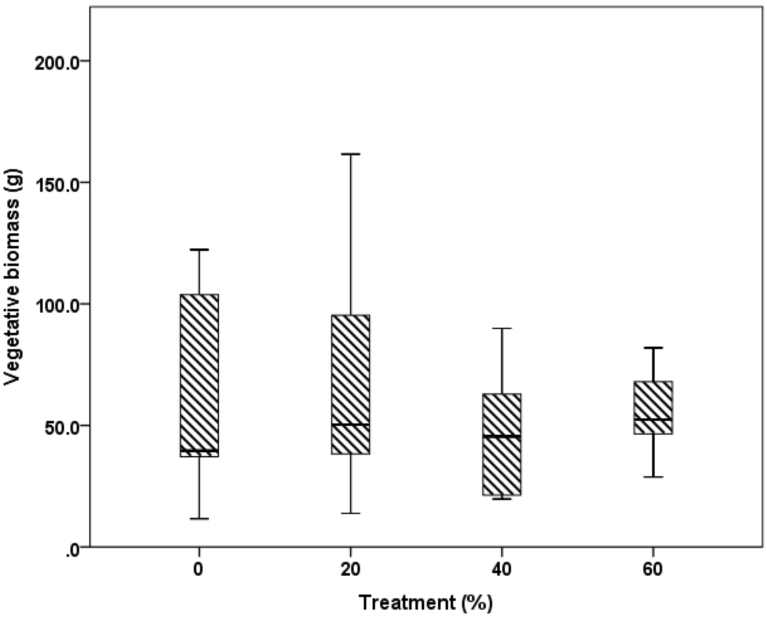


Figure 4. Comparison of a) above-ground and b) below-ground biomass allocation of herbaceous plants across drought treatments.

4.2 Comparison of vegetative and reproductive biomass allocation across drought treatments

The Kruskal - Wallis H test revealed that there was no statistical significant difference between vegetative and reproductive biomass allocation across the drought treatments (H = 0.844, df = 3, p > 0.839). The different levels of drought treatment (0%, 20%, 40%, 60%) do not appear to affect vegetative and reproductive biomass allocation significantly (Figure 5). Across the four drought levels (0%, 20%, 40%, 60% rainfall exclusion), the allocation patterns remained relatively consistent, with slight variations but no clear trend indicating an effect of increasing drought severity.

a)



b)

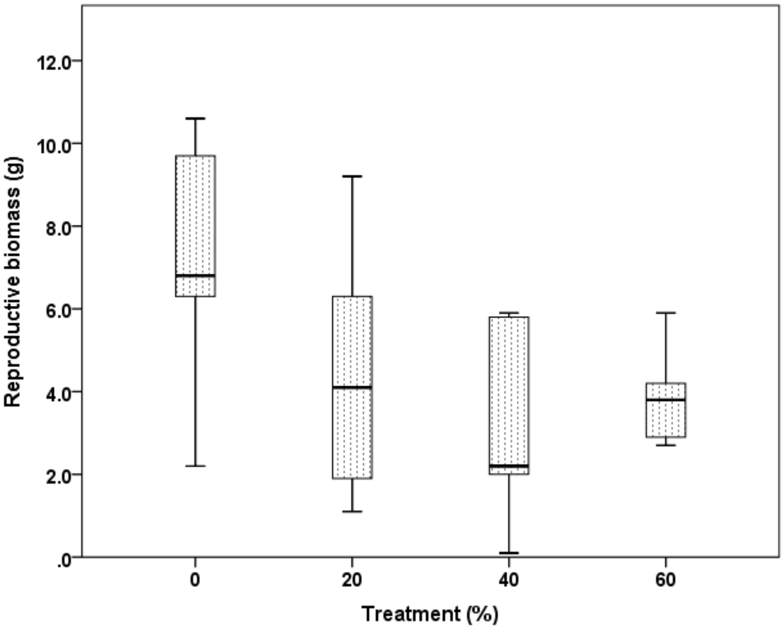


Figure 5. Comparison of a) vegetative and b) reproductive biomass allocation of herbaceous plants across drought treatments.

4.3 Correlation between soil moisture content and biomass allocation

The Spearman's rank correlation analysis showed no significant correlation (r = 0.214, p = 0.366 > 0.05, n = 20) between biomass allocation and soil moisture content (Figure 6). This indicates that biomass allocation was not significantly influenced by the moisture content level across the drought treatments.

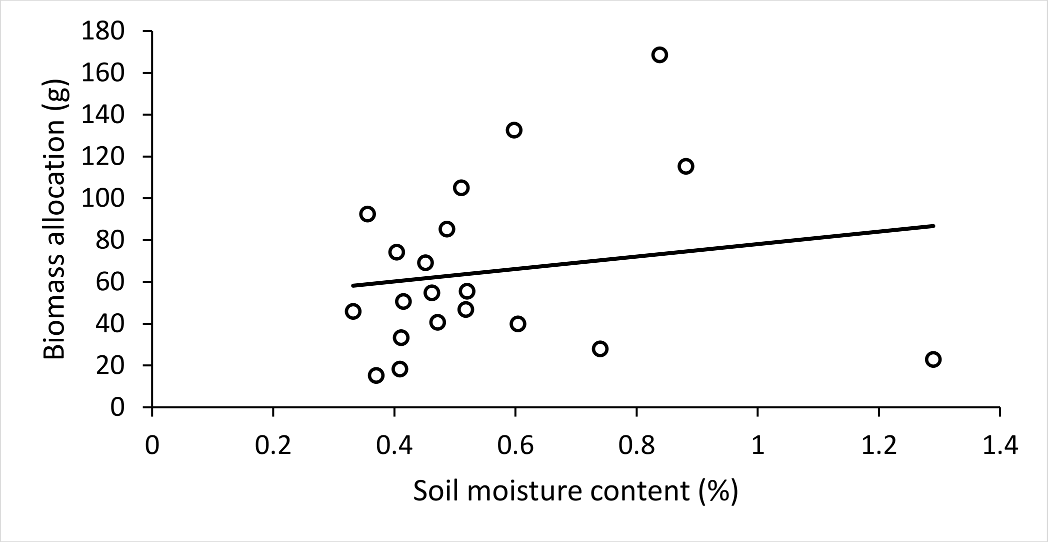


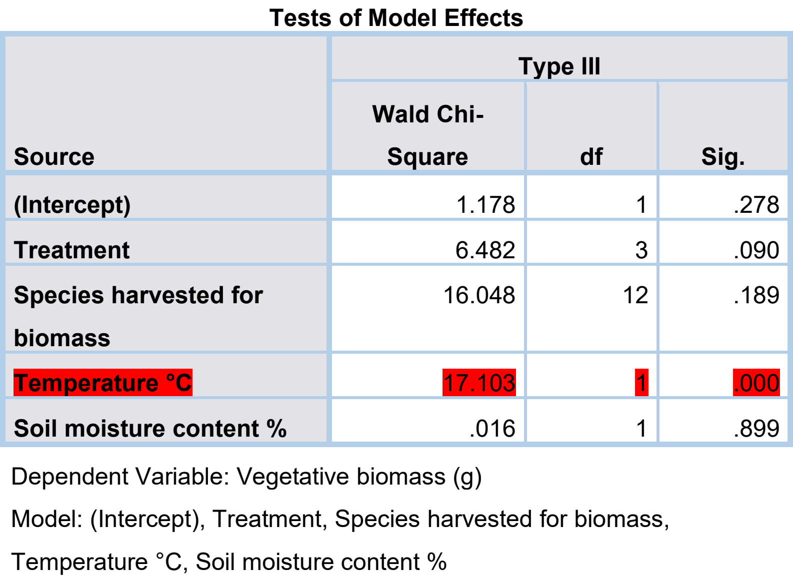
Figure 6. The relationship between soil moisture content (% SMC) and biomass allocation (g/m²).

4.4 Effect of soil, species, temperature and drought treatments on vegetative allocation and reproductive allocation

Effect of soil, species, temperature and drought treatments on vegetative biomass allocation

The Type III Wald Chi-Square test from the Generalized linear models using Gamma distribution revealed that temperature ($\chi2(1) = 17.103$, $p < 0.004$) is a significant predictor of vegetative biomass allocation. While species composition ($\chi2(12), = 16.048$, $p > 0.189$), drought treatment (χ2(3), = 6.482, p > 0.090) and soil moisture (χ2(1), = 0.016, p > 0.899) are not significant predictors in the model (Table 1).

Table 1. The results of the Generalized Linear Model using Gamma distribution with log link function to determine the effect of soil, species, temperature and drought treatments on vegetative biomass allocation.



Tests of Model Effects

	Type III		
Source	**Wald Chi-Square**	**df**	**Sig.**
(Intercept)	1.178	1	.278
Treatment	6.482	3	.090
Species harvested for biomass	16.048	12	.189
Temperature °C	17.103	1	.000
Soil moisture content %	.016	1	.899

Dependent Variable: Vegetative biomass (g)

Model: (Intercept), Treatment, Species harvested for biomass, Temperature °C, Soil moisture content %

Effect of soil, species, temperature and drought treatments on reproductive biomass allocation

The Type III Wald Chi-Square test from the Generalized linear models using Gamma distribution revealed that drought treatment (χ2(3) = 13.114, p < 0.004) is a significant predictor of reproductive biomass allocation. While species composition (χ2(12) = 20.859, p < 0.052), temperature (χ2(1) = 1.525, p < 0.217) and soil moisture (χ2(1) = 2.607, p < 0.106) are not significant predictors in the model (Table 2).

Table 2. The results of the Generalized Linear Model using Gamma distribution with log link function to determine the effect of soil, species, temperature and drought treatments on reproductive biomass allocation.

Tests of Model Effects

	Type III		
Source	**Wald Chi-Square**	**df**	**Sig.**
(Intercept)	2.416	1	.120
Treatment	13.114	3	.004
Species harvested for biomass	20.859	12	.052
Temperature °C	1.525	1	.217
Soil moisture content %	2.607	1	.106

Dependent Variable: Reproductive biomass (g)
Model: (Intercept), Treatment, Species harvested for biomass, Temperature °C, Soil moisture content %

4.5 Effect of shading on photosynthetic capacity of specific herbaceous species across drought treatments

The Friedman Test results indicate that there is a statistically significant difference in chlorophyll content of the selected herbaceous species across the drought treatments ($\chi^2 = 18.456$, df = 1, $p < 0.001$). The herbaceous species showed significant variability in chlorophyll measurements, indicating a diverse response to different treatment levels. *Aptosimum lineare* and *Ocimum americanum* exhibit the highest and most variable chlorophyll levels, especially under treatment 60. In contrast, *Aristida congesta*, *Eragrostis rotifer, Chloris virgata* and *Urochloa brachyura* consistently show low chlorophyll levels across all treatments. Other species (*Chascunum pinnatifidum*, *Melinus* *repens*) have moderate chlorophyll levels with some increase and variability at lower treatments (i.e. 0 and 20 %) (Figure 7).

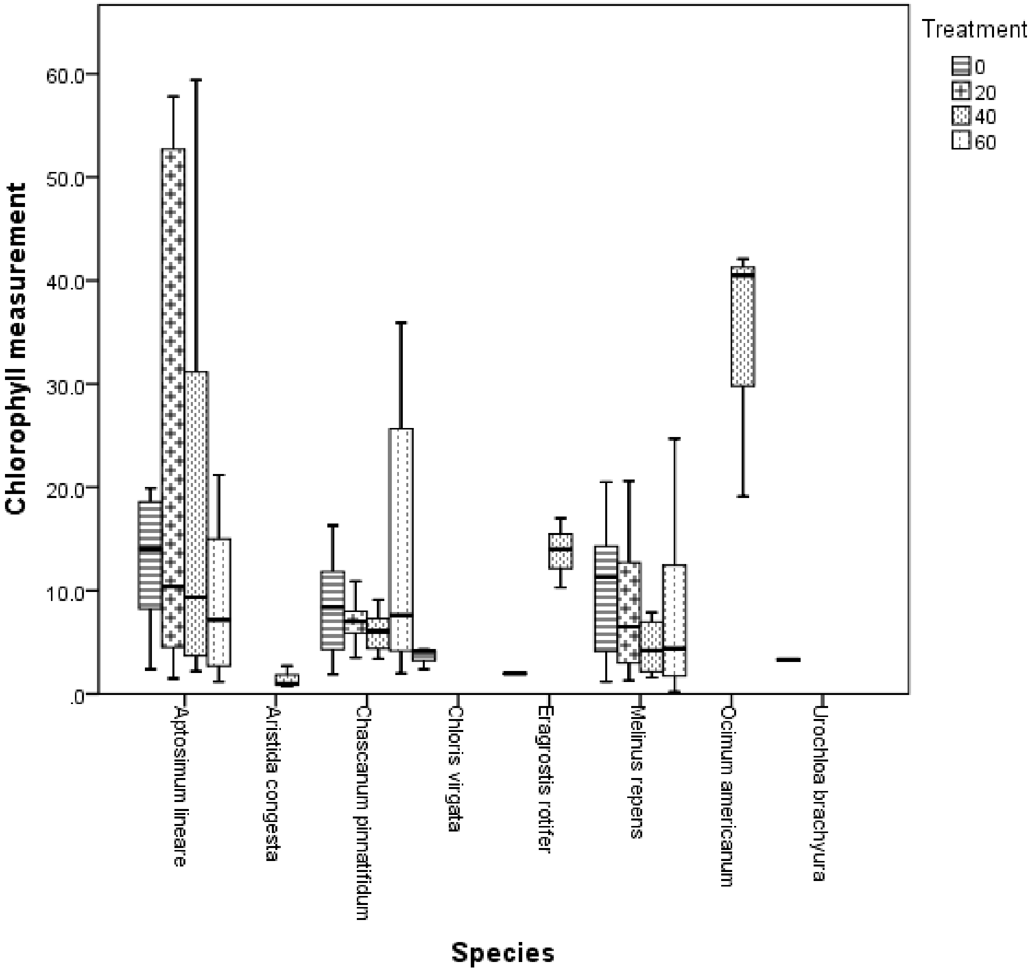


Figure 7. Chlorophyll content measurements across different herbaceous species and drought treatment levels.

4.6 Effect of drought treatment on herbaceous plant cover

The results of the Fisher's exact test revealed that there is no statistical significant association between herbaceous cover classes and drought treatment ($p < 0.724$). The frequencies of cover classes are similar across the different drought treatments. Cover class < 5 consists the majority of observations across all drought treatment levels, with relatively similar frequencies. Cover class 5.1 – 10 consist of the low frequencies across all treatment levels, with slight variations. While Cover class 10.1 - 20 and > 20 have the lowest frequencies across the different drought treatment levels (Figure 8).

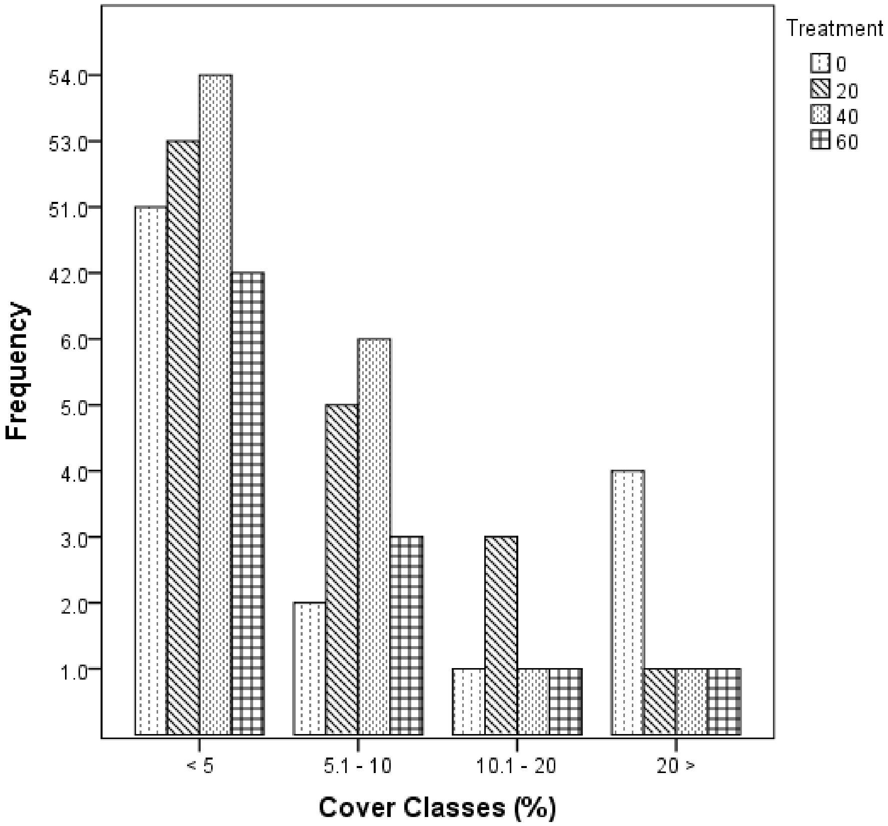


Figure 8. Frequency of herbaceous cover classes (%) across drought treatments.

4.7 Correlation between biomass allocation and herbaceous plant cover

The Spearman's rank correlation revealed no statistically significant correlation ($r = 0.404$, $p = 0.077 > 0.05$, $n = 20$) between biomass allocation and herbaceous plant cover (Figure 9). This indicated that biomass allocation was not significantly influenced by the plant cover.

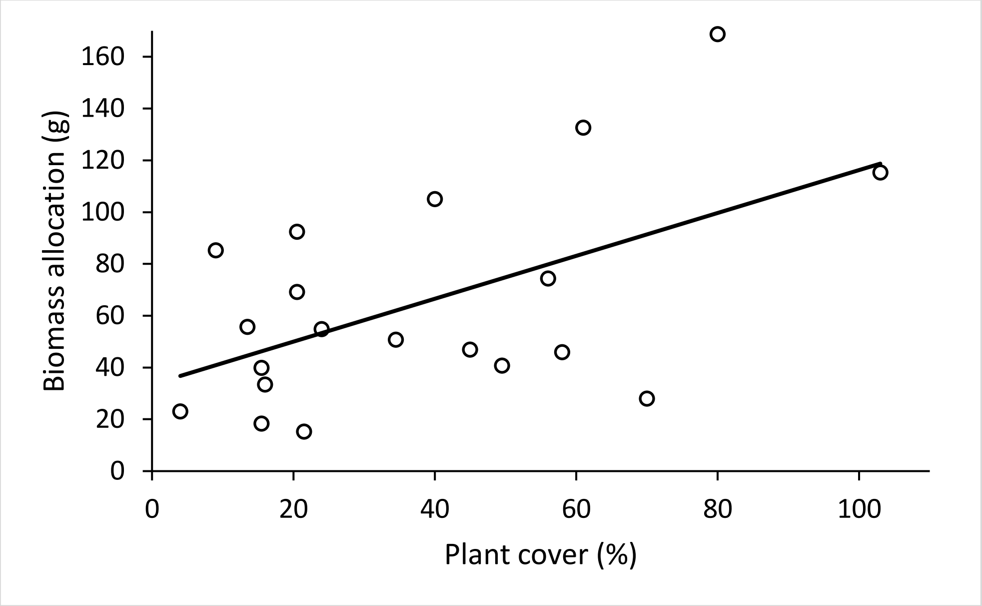


Figure 9. The relationship between herbaceous plant cover and biomass allocation (g).

4.8 Compare species composition of herbaceous species across drought treatments

The Hierarchical Cluster Analysis (HCA) produced 3 clusters at 40% similarity (indicated by the solid black line) in species composition (Figure 10):

Cluster 1 comprised a single plot from the 0% drought treatment, uniquely hosting 2 forb species *Kyphocarpa angustifolia*, *Cyperus fulgens*, and one grass species *Eragrostis rigidior*.

Cluster 2a primarily consisted of plots from the 20% drought treatment, with only one plot each from the 40% and 60% treatments. This cluster had one common herbaceous forb *Aptosimum lineare* and grass *Eragrostis lehmanniana*.

Cluster 2b contained one plot from both the 20% and 40% drought treatments, featuring one common forb *Chascanum pinnatifidum* and the grass *Eragrostis lehmanniana*.

Cluster 2c included two plots from the 60% drought treatment and one each from the 20%, 0%, and 40% treatments, with *Eragrostis lehmanniana* as the common grass species.

Cluster 3a was mainly composed of plots from the 60% drought treatment, along with one each from the 0% and 40% treatments. This cluster shared two grass species, *Melinis repens* and *Pogonarthria fleckii*.

Cluster 3b predominantly consisted of plots from the 0% drought treatment, with one from the 40% treatment. The only common species in this cluster was the grass *Melinis repens*.

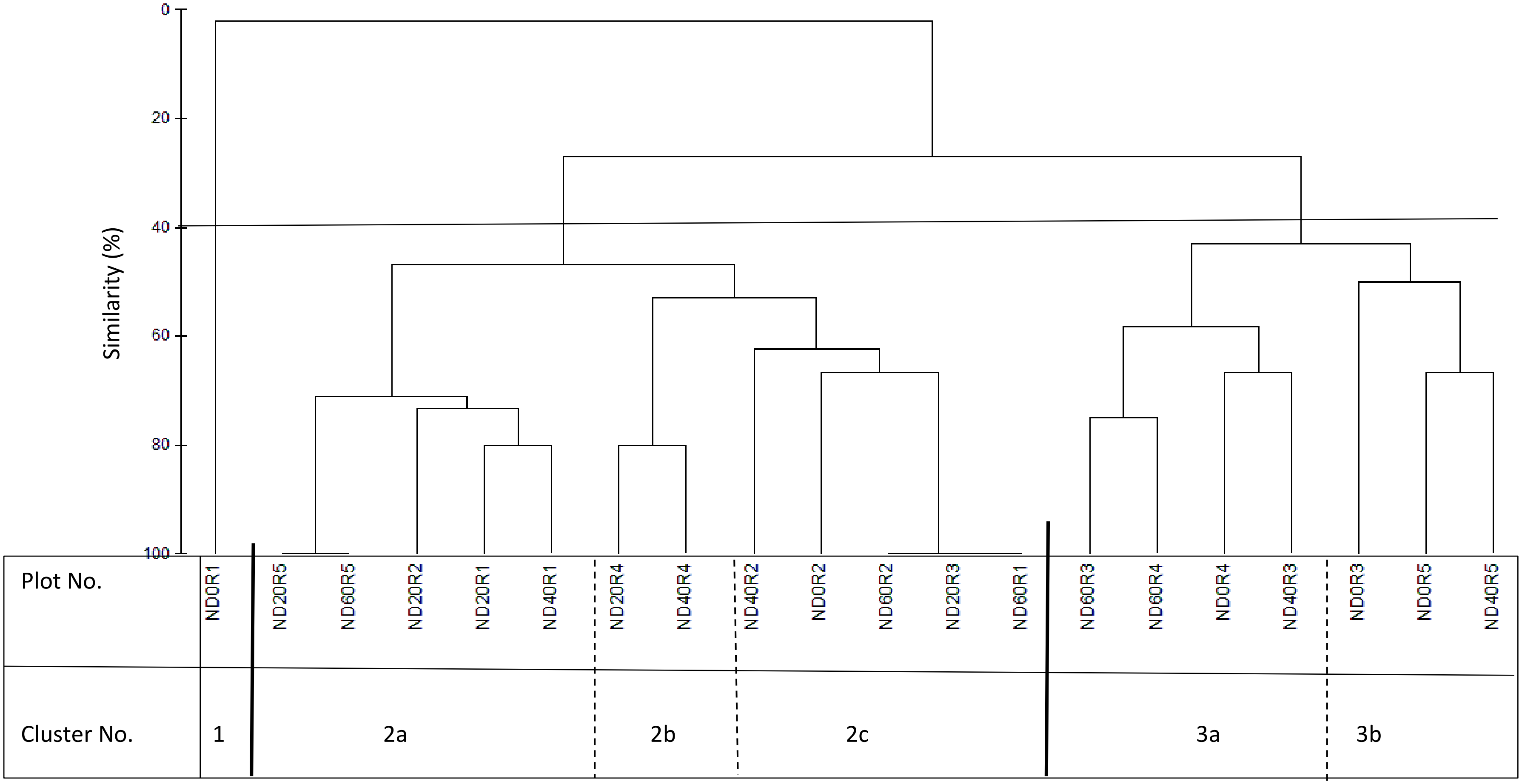

Similarity (%)
0
20
40
60
80
100
Plot No.
ND0R1
ND20R5
ND60R5
ND20R2
ND20R1
ND40R1
ND20R4
ND40R4
ND40R2
ND0R2
ND60R2
ND20R3
ND60R1
ND60R3
ND60R4
ND0R4
ND40R3
ND0R3
ND0R5
ND40R5
Cluster No.
1
2a
2b
2c
3a
3b

Figure 10. Hierarchical Cluster Analysis (HCA) dendrogram showing a classification of herbaceous plant species into 3 clusters based on species presence/absence data. Code key: The first two letters of the code indicate the study site (ND = Neudamm); the first number following the site code represents the drought treatment level (0%, 20%, 40%, 80%); the subsequent letter denotes the replicate of the treatment (R = Replicate) and the final number indicates the replicate number (1, 2, 3, 4, 5).

The Canonical Correspondence Analysis (CCA) separated the plot into 3 groups revealing the distribution of herbaceous species in relation to the selected environmental variables: vegetation biomass (VegBio) and reproductive biomass (RepBio), soil moisture (SoiMoi), temperature (Temp), and drought treatment intensity (Treat) (Figure 11). Axis 1, which accounted for 9.26%, primarily represents the gradient of soil moisture and reproductive biomass. Axis 2 explained 16.60% and reflects the influence of temperature, while Axis 3, associated with drought treatment intensity, accounted for 22.91%. Notably, Axis 4 captured the highest variability at 26.49%, encompassing additional variability not strongly linked to the primary environmental factors (Figure 11). The analysis revealed 3 distinct group were Group 1 included species associated with higher reproductive biomass and soil moisture, such as *Aristida congesta*, *Cyperus fulgens*, and *Eragrostis lehmanniana*. In contrast, Group 2 comprised species linked to higher temperatures, including *Aptosimum lineare, Melinis repens, Schmidtia pappophoroides,* and *Enneapogon cenchroides*. Finally, Group 3 featured species associated with drought treatment intensity, such as *Chascanum pinnatifidum, Aristida meridionalis,* and *Pogonarthria fleckii*.

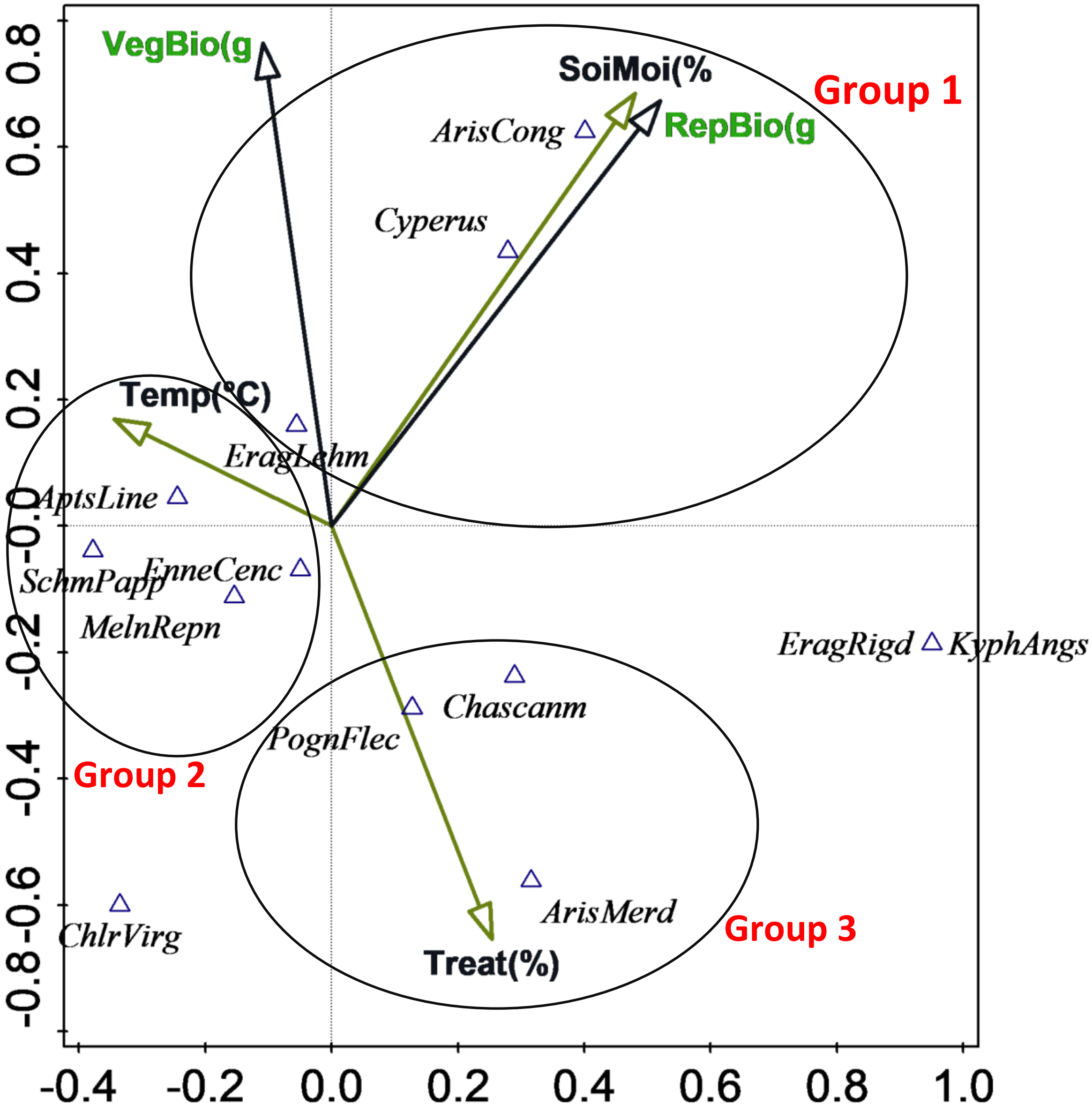


Figure 11. Canonical Correspondence Analysis (CCA) ordination diagram indicating the influence of vegetation biomass (VegBio) and reproductive biomass (RepBio), soil moisture (SoiMoi), temperature (Temp), and drought treatment intensity (Treat) on species composition under rainout shelters at Neudamm agricultural farm.

CHAPTER 5

5. DISCUSSION

5.1 Comparison of above-ground and below-ground biomass allocation across drought treatments.

No significant differences were detected between aboveground and belowground biomass allocation of the herbaceous species across the 4 drought treatments (i.e. 0%, 20%, 40%, 60%) in this study. Our findings are supported by the isometric theory which stipulates that both aboveground and belowground biomass exhibit a proportional relationship, suggesting that there may not be a clear trade-off between these two biomass components (Wang et al., 2014). Moreover, herbaceous plants allocate more biomass to root development during the seedling stage, shifting to increased shoot biomass as they mature to cope with water stress (Qi et al., 2019). Our findings support this, as treatments were applied after the seedling stage and likely did not disrupt the established balance between root and shoot allocation. This equilibrium is vital for optimizing resource use and ensuring survival in arid environments.

Furthermore, Walter et al. (2021) suggested that herbaceous plant roots may not exhibit enhanced growth in response to short-term dryness, which might explain our study's results, as the drought treatment experiment was only conducted for a period of one month. This results are in contrast to findings of empirical studies (Newman et al., 2006; Trillo and Fernandez 2005) which noted that root biomass increases during dry conditions, especially at lower soil depths, thus enhancing root absorption of minerals and water. However, these studies focused on decreased water supply over longer periods rather than over defined periods (Kreyling et al., 2008). Therefore, shorter drought events tend to have no effect on root biomass, whereas longer events generally decrease below-ground biomass (Kreyling et al., 2008).

Gupta et al. (2020) noted that herbaceous species adapt to drought by modifying their root architecture to develop shallow roots for better moisture acquisition. Similarly, Funk et al. (2024) found that under dry conditions, herbaceous plants invest in thin roots with high specific root length (SRL) and specific root surface area (SRSA), rather than relying on thicker roots that depend on mycorrhizal partners. This strategy allows herbaceous species to optimize water uptake without significantly altering the overall biomass allocation between their aboveground and belowground parts. Several species identified in our study, such as *Cenchrus ciliaris* L. and *Eragrostis lehmanniana* Nees., exemplify this trait by investing in efficient root structures while maintaining balanced biomass allocation. This balance is crucial for maximizing resource use efficiency and enhancing survival under drought conditions, as demonstrated by the adaptations of these species (Asefa et al., 2022; Marshall, Lewis, and Ostendorf, 2012; Cable, 1971).

Furthermore, the absence of a clear trade-off between aboveground and belowground biomass allocation may be due to the grouping of species for assessing allocation patterns. This study did not separate or individually evaluate each species, which could obscure their distinct responses to drought stress. This approach could make it challenging to discern specific allocation strategies among different species. Research by Eziz et al. (2017) highlights that perennial herbaceous plants, such as *Aptosimum lineare*, *Aristida meridionalis*, and *Eragrostis lehmanniana*, which were found to be abundant at our study area, are generally less sensitive to drought stress compared to annual species like *Chloris virgata* and *Melinis repens*. Perennials tend to invest in adaptations that enhance their resilience over multiple growing seasons, while annuals often prioritize immediate reproduction and growth (Eziz et al., 2017). This difference in strategy leads annual plants to allocate less biomass to storage and defense mechanisms, making them more vulnerable to abiotic stresses. Moreover, under drought conditions, perennial plants may exhibit a slight increase in aboveground biomass compared to annuals, which could be attributed to differences in ontogeny and plant size (Poorter et al., 2012). This suggests that while individual species might show varied responses, the overall pattern of biomass allocation does not significantly differ between aboveground and belowground components when viewed collectively.

The absence of a trade-off between belowground and aboveground biomass allocation indicates that herbaceous plants can sustain essential ecosystem functions even when under stress in arid regions. This insight can inform conservation strategies focused on preserving nutrient cycling, soil health, and overall ecosystem productivity. This understanding can inform conservation strategies and habitat restoration by prioritizing drought-resistant perennials like *Cenchrus ciliaris* and *Eragrostis lehmanniana* to bolster ecosystems' resilience to climate variability. Furthermore, the results suggest that herbaceous plants may not show increased root growth in response to short-term droughts, underscoring the need for effective water resource management, especially in areas where these plants play a vital role in soil stabilization and water retention.

5.2 Comparison of vegetative and reproductive biomass allocation across drought treatments

Water deficits influence the vegetative and reproductive biomass of herbaceous plants, with the degree of impact largely depending on the timing, duration, and frequency of drought stress (Moolman et al., 1996). In terms of drought duration, Poorter et al. (2012) suggested that herbaceous plants may not respond strongly to relatively short periods of drought, as water availability often hinges on unpredictable rainfall events. Rapidly changing biomass allocation in response to such short droughts could lead to suboptimal growth once water supply is restored (Poorter et al., 2012). This may explain why the drought experiment in this study, which lasted only one month, might have been insufficient for noticeable differences in vegetative and reproductive biomass allocation to emerge.

Herbaceous plants that exhibit minimal trade-offs in terms of vegetative and reproductive biomass allocation during drought stress are typically classified as drought-tolerant (Yin et al., 2019). In line with this, an increase in root mass fraction which serves as a water uptake strategy, is known to allow these plants to maintain both their overall growth and reproductive success even in conditions of water scarcity (Eziz et al., 2017). Additionally, herbaceous species exhibit less sensitivity in their reproductive allocation, demonstrating resilience through their capacity to dynamically adjust growth strategies in response to varying environmental conditions (Yin et al., 2019). This adaptability contrasts with woody plants, which tend to significantly decrease reproductive biomass during drought. Species found at the study site such as *Chloris virgata, Aristida congesta, Schmidtia pappophoroides, Melinis repens, Pogonarthria fleckii,* and *Eragrostis lehmanniana* revealed to be drought tolerant and hence balancing allocation patterns between reproductive and vegetative could be an adaptation mechanism.

It is important to note that again the assessment of vegetative and reproductive biomass allocation was conducted by grouping all species together without individual evaluations.

This methodology may have obscured species-specific traits and responses to drought stress, making it challenging to identify distinct allocation strategies among different species. In support of the latter, under drought conditions, some herbaceous plants typically reduce their reproductive investment due to the high energy and water demands of reproductive processes (Eziz et al., 2017). This reduction is often a response to declines in photosynthesis and changes in phenology, leading to decreased biomass allocation to reproductive structures. Some herbaceous plants may adapt to drought by undergoing phenotypic changes, such as producing fewer and smaller flowers and shallower nectar tubes. These adaptations could impact pollinator attraction and ultimately lead to reduced reproductive output (Kuppler et al., 2021). Supporting this, Zia et al. (2021) noted that limited water availability restricts photosynthesis, resulting in fewer resources for reproduction and flower production. Thus, while individual species might exhibit varied responses to drought conditions, the overall pattern of biomass allocation might not show significant differences between vegetative and reproductive components when viewed collectively. Ecologically, intense water scarcity may lead to shifts in community structures by favoring drought-tolerant species, resulting in changes in species composition that disrupt existing ecological relationships and interactions.

In this study, an increase in drought stress led to a reduction in both vegetative and reproductive biomass allocation. This provides compelling evidence that drought stress significantly impacts biomass distribution. Studies have revealed simultaneous decline in vegetative and reproductive biomass under drought stress is driven by a reduction in leaf area, which can decrease by over 60% during drought (Bistgani et al., 2024), as well as reduced photosynthetic capacity due to diminished photosynthetic pigments and damage to mesophyll tissue (Eziz et al., 2017). These changes reflect the plant's adaptive strategies to cope with water scarcity but ultimately compromise its growth and reproductive output. Furthermore, the concurrent decline in both vegetative and reproductive biomasses can destabilize ecosystems, especially in semiarid regions where herbaceous plants are essential for maintaining soil health and preventing erosion. This decline may result in increased soil degradation and increased susceptibility to erosion, ultimately affecting the overall health of these ecosystems.

5.3 Correlation between soil moisture content and biomass allocation

Soil moisture content is amongst the key factors controlling plant growth and resource allocations in semiarid regions. The availability of soil moisture content profusely governs plant water relations which directly impacts stomatal conductance and photosynthesis (Vennam et al., 2023). Soil moisture content was found to have no correlation with herbaceous biomass allocation suggesting that herbaceous plants might have maintained a relatively stable allocation strategy despite varying soil moisture levels. Studies have suggested that drought stress may not significantly impact the scaling exponents of allometric relationships between herbaceous plant tissues, indicating that these inherent allocation patterns remain stable despite changes in moisture availability (Eziz et al., 2017; Liu et al., 2021). Consistent with this observation, Eziz et al. (2017) noted that during periods of environmental constraint, plants tend to adhere to a specific allometric trajectory. This preference for a simplified allometric strategy is often more advantageous than adopting complex and varied trajectories based on the availability of specific resources.

Increased soil moisture typically enhances nutrient availability, allowing plants to allocate more resources to both root and shoot growth. However, under drought conditions, plants may respond uniformly by reducing nutrient content in both above- and below-ground organs to maximize adaptability (Liu et al., 2021). This coordinated reduction can obscure any direct correlation with soil moisture content since all plant parts are affected similarly. In addition, Herod and Martina (2024) found that the stem-to-leaf ratio in herbaceous plants increases with higher soil moisture content. However, during drought, this ratio may not change significantly if both stem and leaf growth are constrained equally.

While decreased soil moisture modifies plant-soil feedback effects on biomass allocation, these modifications may not significantly impact overall plant performance (de Vries et al., 2023). Therefore, even if plants adjust their biomass allocation strategies under drought stress, these adjustments might not lead to observable differences in allocation patterns when moisture is limited. The absence of significant differences between reproductive and vegetative biomass allocation suggests that under drought stress, plants may prioritize resource allocation differently. While adequate moisture supports optimal photosynthesis and increases leaf area (Wang et al., 2022), drought conditions force plants to focus on survival mechanisms rather than growth, leading to a more uniform allocation strategy across different plant parts (Gao et al., 2010).

Furthermore, different herbaceous species exhibit varying responses to drought stress, with some allocating more resources to root growth while others prioritize aboveground biomass for photosynthesis and reproductive success (Eziz et al., 2017). In the context of this study, which combined all species for biomass allocation analysis, this variability could have influenced the results. Given that species possess different sensitivities to drought, the overall findings may not reveal significant differences in biomass allocation patterns, even when soil moisture levels fluctuate (Li et al., 2021). This variability complicates the establishment of a direct correlation between biomass allocation and soil moisture content.

As previously mentioned, the timing and duration of drought stress can significantly impact biomass allocation patterns. Short-term droughts often prompt immediate adjustments in biomass allocation that may not accurately reflect long-term soil moisture conditions (Eziz et al., 2017). This aligns with the current study, as the drought treatments were implemented for only one month. Consequently, the observed allocation patterns may not correlate with soil moisture levels due to the temporal nature of plant responses.

The maintenance of stable biomass allocation strategies despite fluctuations in soil moisture levels suggests that these species exhibit resilience, enabling them to thrive in variable environments and ensuring their persistence and ecological roles in semiarid regions. Additionally, the inherent stability in their allocation patterns indicates that they will continue to support essential ecosystem functions, such as soil stabilization and nutrient cycling, even during periods of stress, thereby contributing to overall ecosystem resilience. Furthermore, the observed variability in species responses to drought stress implies that certain species may be better equipped to handle water scarcity than others. This could result in shifts in community composition over time, influencing competition dynamics and overall biodiversity within ecosystems. Therefore, it is crucial to identify how species allocate resources differently under drought conditions to help inform conservation strategies aimed at prioritizing the protection of more resilient species, ultimately enhancing ecosystem stability and functionality.

5.4 Effect of soil, species, temperature and drought treatments on vegetative allocation and reproductive allocation

Temperature was determined to be the strongest predictor of vegetative biomass compared to soil moisture content, species present and drought treatment. Rainout shelters can significantly impact temperature compared to ambient conditions as they can increase temperatures under the shelter by 1.2-1.8°C on average (Balota, 2020). A global meta-analysis revealed that rising temperatures impact biomass allocation in terrestrial plants, causing them to allocate more biomass to vegetative growth as a strategy for survival (Zhou et al., 2022). In consistent with our findings, temperature was shown to have a positive correlation with vegetative biomass, as all physiological processes and biochemical reactions in plants require suitable temperature conditions to occur efficiently (Zhao et al., 2024). In support of the aforementioned findings, a study has demonstrated that plant cover and species richness exhibit significant sensitivity to increases in temperature, potentially leading to drastic reductions under elevated thermal conditions (Yao et al., 2022). Both plant cover and species richness are closely associated with vegetative biomass, thereby highlighting the substantial influence of temperature on vegetative biomass dynamics. Additionally, elevated temperatures can reduce the root absorption area, potentially impacting growth patterns, survival, and adaptation (Zhao et al., 2024).

The lack of significance for species composition may be explained by the finding that while different species may respond differently to environmental conditions, the overarching effect of temperature on biomass allocation can overshadow these differences. Moreover, species composition alone may not yield significant insights into vegetative biomass allocation due to its failure in accounting for the specific functional traits, physiological processes, and environmental responses of individual species, which possess distinct strategies for biomass distribution (Eziz et al., 2017). Therefore, understanding biomass allocation necessitates a focus on species-specific traits such as root-to-shoot ratios, growth rates, and adaptive responses rather than solely on species composition (Garnier et al., 2004; Wright et al., 2004). Similarly, the non-significant effects of drought treatment and soil moisture suggest that while these factors are important, they may not directly influence biomass allocation as strongly as temperature does. As mentioned in the analysis of biomass allocation versus soil moisture, it is noted that soil moisture may not directly influence biomass allocation due to factors such as the duration of the study, the clumping of different species, and the maintenance of specific allometric trajectories. These factors could help explain why soil moisture was not identified as a significant predictor of vegetative biomass.

Furthermore, drought treatment was found to be a significant predictor of reproductive biomass allocation compared to soil moisture content, species and temperature. As previously stated, rainout shelters modify the microclimate of the species beneath them, leading to changes in temperature and solar radiation, both of which are crucial for plant reproduction (Thaler et al., 2023). Eziz et al. (2017), alluded that herbaceous species under drought stress reduce reproductive investment due to decreased photosynthesis and altered phenology, which significantly lowers biomass allocation to reproductive parts. In support, a study using rain-out shelters found that seed biomass in drought-stressed plants was 65% lower than in controls, while total biomass decreased by 35-50%, highlighting that the disproportionate reduction in reproductive biomass suggests plants prioritize survival over reproduction under drought conditions (Ploschuk et al., 2005).

Moreover, meta-analyses have shown that drought stress typically decreases the mass fraction of reproductive tissues while increasing root mass, indicating a shift in resource allocation towards survival rather than reproduction (Eziz et al., 2017). It has also been noted that rain-out shelter drought treatments can affect reproductive allocation differently in annual and perennial species. In line with this, a studies have found that reproductive allocation in perennial herbs was more sensitive to drought than in annual herbs, despite annuals experiencing greater reductions in total biomass (Ploschuk et al., 2005, Eziz et al., 2017). This aligns with our study, as most of the herbaceous species under the rain-out shelters were perennials, which explains why the treatments may be more significant predictors in our findings.

The lack of significance of species composition in reproductive biomass allocation may be due to the fact that different species respond differently to environmental factors. Species-specific adaptations and strategies for biomass allocation under drought conditions can overshadow the influence of species identity (Wilschut and van Kleunen, 2021). This variability can weaken the predictive power of species composition as a factor in reproductive biomass allocation. Similarly, temperature and soil moisture content were found to be not significant predictors of reproductive biomass. In many cases, plants tend to respond more to moisture availability than to temperature changes, particularly when it comes to reproductive strategies under drought conditions (Brown et al., 2022). Moreover, a study found that while soil moisture affects overall biomass, it did not significantly influence the allocation specifically to reproductive structures when drought was a factor (Wilschut and van Kleunen, 2021).

The identification of temperature as the primary predictor of vegetative biomass suggests that increasing global temperatures may lead to a greater allocation of biomass towards vegetative growth. This trend could enhance plant survival in warmer climates but may also disrupt community dynamics, potentially resulting in the dominance of heat-tolerant species. As warming affects biomass allocation patterns across different biomes, it could lead to a homogenization effect, where biodiversity is reduced as similar species adapt in analogous ways to rising temperatures. Such changes could ultimately undermine ecosystem resilience and stability. Moreover, the complex interactions between temperature, species, soil moisture, and biomass allocation underscore the need for long-term ecological monitoring. Such studies can provide valuable insights into how ecosystems will respond to ongoing climate change, informing effective management and conservation strategies.

5.5 Effect of shading on photosynthetic capacity of specific herbaceous species across drought treatments

Chlorophyll content is vital for sustaining photosynthetic capacity, as it plays a key role in photosynthesis by absorbing, distributing, and converting light energy (Turan and Tripathy, 2015). It is often closely linked to the photosynthetic rate and the accumulation of organic matter (Qi et al., 2019). Drought stress reduces the photosynthetic rate by altering chlorophyll content, affecting its components, and damaging chloroplasts through reactive oxygen species (Mafakheri et al., 2010). Mafakheri et al. (2010) further noted that drought stress during the vegetative stage significantly reduced chlorophyll a, chlorophyll b, and total chlorophyll content at both the vegetative and flowering stages, while drought stress at anthesis also impacted these contents at flowering due to a reduced capacity for light harvesting. To add on, the reduction in chlorophyll content can be regarded as a common symptom of oxidative stress, resulting from pigment photo-oxidation and chlorophyll breakdown (Talbi et al., 2020). The findings mentioned above demonstrate how drought treatment affects chlorophyll content in herbaceous species, thereby supporting our results which found a significant direct relationship between chlorophyll levels and drought treatment.

Chlorophyll content in the selected herbaceous species differed significantly across drought treatments, indicating that these species showed varied responses to different levels of drought stress in terms of chlorophyll levels. Species such as *Aptosimum lineare* and *Ocimum americanum* exhibit the highest and most variable chlorophyll levels, especially under treatment 60 that could imply that these species are well-suited for growth in the conditions provided by this treatment. The above mentioned species are known to be medicinal and aromatic plants which are known to possess the ability to thrive in harsh environmental conditions, particularly drought, making them well-suited for arid regions (Bistgani et al., 2024). Additionally, as drought stress intensifies, the amount of chlorophyll b increases, enabling medicinal plants to better withstand dry conditions by boosting photosynthesis and improving food processing efficiency (Bistgani et al., 2024). Hence *Aptosimum lineare* and *Ocimum americanum* exhibit drought tolerance traits under drought stress as they are known to regulate stomatal conductance to minimize water loss, adjust photosynthetic rates to optimize energy utilization under water-limited conditions and undergo morphological adaptations such as reducing leaf area and deepening root systems to enhance water absorption (Nazari et al., 2023). Chlorophyll content is indicated by the greenness of leaves; thus, increased leaf greenness reflects higher total chlorophyll levels, which in turn boosts the rate of photosynthesis (Syamsia et al., 2018). This was observed in this two perennial species that exhibited greener leaves under rainout shelters compared to other species. Their ability to maintain higher chlorophyll levels suggests resilience, enabling them to perform photosynthesis effectively even when water is limited which better enhances their survival rates in arid environments. The latter is critical for maintaining biodiversity in ecosystems facing increased drought frequency due to climate change.

In contrast, *Aristida congesta*, *Eragrostis rotifer*, *Chloris virgata* and *Urochloa brachyura* consistently show low chlorophyll levels across all treatments which means that their photosynthesis capacity is greatly impacted by drought. The low levels of chlorophyll content could be due to stress-induced changes in the synthesis of chlorophyll precursors or increased chlorophyll breakdown by chlorophyllase (Bistgani et al., 2024). Additionally, another significant reason for the reduction in chlorophyll levels under drought stress is the increase in O2− and H2O2, which promotes lipid peroxidation and leads to chlorophyll degradation (Kapoor et al., 2020). A decrease in leaf water content can also slow down the rate of chlorophyll synthesis while accelerating chlorophyll degradation. Moreover, the consistently low chlorophyll levels suggest that these plants may be more vulnerable to drought stress, which could limit their distribution and abundance in changing environments. Other species (*Chascunum pinnatifidum, Melinus repens*) have moderate chlorophyll levels with some increase and variability at lower treatments (i.e. 0 and 20 %). Such variability suggests that while drought stress might impact overall biomass allocation, these species can still maintain moderate chlorophyll levels as a strategy for survival and reproduction in challenging conditions. The variability in chlorophyll content among species under drought conditions underscores the need for long-term ecological monitoring to understand how plant communities will respond to ongoing climate change. Such research is vital for developing effective management strategies to enhance ecosystem resilience.

5.5 Effect of drought treatment on herbaceous plant cover

Herbaceous plant cover was found to be not significantly associated with drought treatment, indicating that the drought treatments did not significantly impact cover levels. This phenomenon can be attributed to the resilience of several herbaceous species found under the rainout shelters, including *Aptosimum lineare, Aristida meridionalis, Chascanum pinnatifidum, Pogonarthria fleckii, Eragrostis lehmanniana,* and *Schmidtia pappophoroides*, which are capable of maintaining cover despite variations in water availability. Such resilience can lead to stable herbaceous cover across different drought treatments, resulting in no significant differences observed (Ebel et al., 2022). Additionally, the reduction in herbaceous cover may vary between perennials and annuals, with annuals expected to decrease in cover more quickly than perennials under drought stress. This was supported by a study (Smit et al., 2024) that found annual grasses declined in cover and productivity much faster than perennial grasses during drought conditions, while the decline in perennials was more gradual but consistent. Additionally, the temporal dynamics of drought effects may explain these findings, as the impacts of drought might not be immediately reflected in herbaceous cover (Ebel et al., 2022). It has been observed that savanna vegetation often experiences a delayed response to reduced rainfall, with changes not always occurring immediately (Smit et al., 2024). This could explain the findings, as the shelters were only in place for a month, which may not have been a sufficient duration for drought stress to impact the herbaceous species cover.

Across the drought treatments, cover class < 5 consists the majority of observations across all drought treatment levels, with relatively similar frequencies which implies that a significant portion of the herbaceous community is characterized by low vegetation cover. The primary reason for this observation is water limitation resulting from the use of rainout shelters. Although soil moisture content was not statistically different across the drought treatments, it was observed to decrease with increasing drought stress. This indicates that the vegetation under the shelters experienced similar soil moisture limitations, regardless of the specific drought treatment applied. The reduction in soil moisture content across the drought treatments likely contributed to the herbaceous species adapting to maintain low cover levels as a survival strategy in response to water stress (Ebel et al., 2022). By reducing their cover, these species can conserve resources and minimize water loss, enabling them to withstand the imposed drought conditions. Another contributing factor to the dominating low vegetation cover could be that the herbaceous species present are resilient to varying levels of drought stress as discussed before. Despite the differences in water availability, these species are able to maintain low cover levels, which may be a strategy to conserve resources during periods of water scarcity (Ebel et al., 2022; Tilman & Downing, 1994).

The herbaceous cover class 5.1 – 10 consisted of the low frequencies across all treatment levels, with slight variations. While Cover class 10.1 - 20 and > 20 have the lowest frequencies across the different drought treatment levels. This distribution suggests that the majority of herbaceous species are unable to achieve higher cover levels under the imposed drought conditions, indicating a potential limitation in growth and cover due to water stress. The low cover levels observed suggest that herbaceous species are employing resource conservation strategies in response to water stress (Eziz et al., 2017). This behavior aligns with findings that drought conditions often lead plants to increase root mass while reducing leaf and reproductive mass, indicating a shift in biomass allocation towards survival rather than growth (Eziz et al., 2017). In support of the latter, water stress not only limits individual plant growth but also affects community structure and diversity (Johnson & Fletcher, 2023).

5.6 Correlation between biomass allocation and herbaceous plant cover

The study found no correlation between herbaceous biomass allocation and plant cover. This lack of correlation may stem from the diverse responses of different herbaceous species to drought stress, resulting in inconsistent relationships between biomass allocation and plant cover. Previous research has indicated that specific leaf area (SLA) can positively correlate with aboveground biomass in certain plant species, suggesting that higher biomass can lead to increased leaf area and, consequently, greater plant cover (Sun et al., 2017). However, this correlation is often species-specific, and not all genera exhibit a strong relationship between SLA and biomass (Sun et al., 2017). The grouping of species for biomass allocation analysis may have obscured these specific results. This means that while individual species may respond differently in terms of biomass allocation, these variations were not captured since they were not assessed separately. For instance, *Aptosimum lineare* may maintain a higher SLA under moderate drought conditions, allowing it to enhance light capture and sustain productivity. In contrast, *Aristida meridionalis* and *Eragrostis lehmanniana* might show lower SLA during severe drought, reflecting a strategy aimed at reducing water loss and adapting to resource-limited environments.

Moreover, biomass allocation trade-offs, such as those between roots and shoots, can influence plant cover differently based on species, growth stages, developmental phases, and environmental conditions (Zhou et al., 2022; Bektas et al., 2023). For instance, plants may invest more in root biomass to enhance water and nutrient uptake during periods of water scarcity, while others may prioritize shoot growth to maximize light capture (Yang and Russo, 2024). This trade-off can vary significantly among species, with some exhibiting greater adaptability to changing environmental conditions than others. Moreover, the complexity of these trade-offs is further emphasized by the multidimensional nature of resource allocation strategies, which can include considerations of mycorrhizal associations that facilitate nutrient acquisition (Yang and Russo, 2024). This suggests that while there is a tendency for increased biomass to enhance cover, the variability introduced by external conditions such as soil moisture, microbial activities and drought can weaken the correlation. Hence the correlation between biomass allocation and plant cover might not be as straightforward, which could explain the none correlation found in this study.

The absence of a clear relationship between biomass allocation and plant cover may indicate that some species are better suited to thrive under drought conditions, potentially leading to shifts in community composition. As more drought-tolerant species become dominant, this could reduce biodiversity and alter ecosystem functions. Identifying species with strong drought tolerance traits can inform conservation strategies aimed at preserving biodiversity in arid regions. Protecting these resilient species will enhance ecosystem stability and functionality amidst climate variability.

5.7 Compare species composition of herbaceous species across drought treatment

Species composition in herbaceous communities revealed significant relationships with biomass allocation and chlorophyll content, particularly under varying drought conditions. The Hierarchical Cluster Analysis (HCA) revealed three distinct clusters at a 40% similarity threshold in species composition, reflecting the performance of herbaceous species under drought stress caused by the rainout shelters. Cluster 1 was notably isolated from the other clusters and consisted of three unique species: *Kyphocarpa angustifolia, Cyperus fulgens,* and *Eragrostis rigidior*. The presence of these species exclusively in a control plot (i.e., a non-drought plot) suggests that they thrive best in conditions with adequate soil moisture, sufficient precipitation, and favorable temperatures (Wang et al., 2014). This finding aligns with ecological principles indicating that certain species are adapted to specific moisture regimes as for instance, *Cyperus fulgens* is recognized as a water-loving perennial, typically found in wetland areas or locations with consistently moist soil conditions (Tropical Plants Database, n.d.). Its presence under a shelter that was found to have a small pit that retains water, further supports the notion that these species require a moist environment to flourish. Moreover, *Kyphocarpa angustifolia* is known for its ability to survive in moist habitats, reinforcing the idea that these species are specialized for environments where water is slightly abundant.

Clustering of plots based on species composition provides valuable insights into the resilience and adaptability of plant communities to varying levels of drought stress. Clusters 2a, 2b, and 2c represent a gradient of drought tolerance. Species in Cluster 2a, such as *Aptosimum lineare*, are adapted to moderate drought conditions, demonstrating drought tolerance that enables them to thrive in areas with moderate water availability (Mongalo & Makhafola, 2018). In contrast, Cluster 2b includes species that can tolerate more severe drought, such as *Chascanum pinnatifidum*, which is recognized as a drought-tolerant forb species capable of thriving in semi-arid environments. Its ability to persist in both the 20% and 40% drought treatment plots indicates a degree of plasticity in response to water availability (Du Preez, 2012). Moreover, the presence of *Eragrostis lehmanniana* across multiple sub-clusters (2a, 2b, and 2c) underscores its adaptability to varying moisture levels, as it can extract moisture even when soil water content is extremely low (Buerdsell & Lehnhoff, 2023). This adaptability suggests that *Eragrostis lehmanniana* plays a crucial role in maintaining community structure under drought conditions, highlighting its potential as a keystone species in arid and semi-arid ecosystems.

The predominance of plots from the 60% drought treatment in Cluster 3a highlights that the species within this cluster are adapted to withstand severe drought conditions. *Melinis repens* and *Pogonarthria fleckii* are recognized for their resilience and ability to thrive in arid environments, making them well-suited to survive in conditions where water availability is significantly limited (Gutiérrez-Gutiérrez et al., 2023). In contrast, Cluster 3b predominantly consisted of plots from the 0% drought treatment, with one plot from the 40% treatment, where the only common species was *Melinis repens*. The presence of *Melinis repens* in both clusters indicates its versatility and adaptability to different moisture regimes, allowing it to thrive in both well-watered and drought-stressed environments. This adaptability underscores the ecological significance of *Melinis repens*, as it can effectively occupy varied habitats and contribute to ecosystem stability across different moisture conditions.

In terms of biomass allocation under drought stress, the findings of this study align with existing literature. Under moderate drought stress (Cluster 2), species such as *Aptosimum lineare* and *Eragrostis lehmanniana* maintain a balance between vegetative and reproductive biomass to ensure survival and reproduction in limited water availability. In contrast, under severe drought conditions (Cluster 3), species like *Melinis repens* and *Pogonarthria fleckii* may prioritize vegetative growth over reproduction to enhance their chances of survival. This prioritization is supported by research indicating that plants often allocate more resources to root development during drought to maximize water uptake, thereby sacrificing reproductive structures (Eziz et al., 2017). The ability to adapt biomass allocation strategies in response to varying drought conditions confirms the resilience of these species and their ecological significance in maintaining community structure under stress.

The findings from the Canonical Correspondence Analysis (CCA) provide vital insights into how herbaceous species distribute themselves in relation to various environmental variables. Group 1 consisted of *Aristida congesta*, *Cyperus fulgens*, and *Eragrostis lehmanniana* which are known to be drought-tolerant species that thrive in arid and semi-arid environments. Their association with higher reproductive biomass and soil moisture suggests that these species have adapted to utilize available resources efficiently, particularly in areas with limited water availability. Some herbaceous species are linked to reproductive biomass and soil moisture due to their physiological adaptations and ecological requirements. For instance, studies have indicated that higher soil moisture levels correlate with increased plant height, leaf area, and overall biomass, which directly supports reproductive success (Liu et al., 2021; Asfaw, Zewedu and Usmane., 2020; Chadha et al., 2019). Conversely, when faced with soil moisture stress, these plants often experience reduced cell enlargement and metabolic activities, leading to a decline in reproductive biomass. This stress can trigger physiological responses such as stomatal closure and altered carbon partitioning, further limiting their ability to reproduce effectively (Chadha et al., 2019). Thus, the availability of soil moisture plays a crucial role in shaping the growth dynamics and reproductive strategies of herbaceous species, highlighting their adaptability to varying environmental conditions.

Group 2 comprised species linked to higher temperatures, including A*ptosimum lineare, Melinis repens, Schmidtia pappophoroides*, and *Enneapogon cenchroides*. This implies that these species are adapted to higher temperatures. Various herbaceous species, including those in Group 2, may exhibit enhanced growth rates at higher temperatures, leading to greater biomass production. This is particularly evident in grasses like *Melinis repens* and *Schmidtia pappophoroides*, which thrive in warm conditions and can dominate grassland ecosystems (Mogonong et al., 2023). By visually observations, *Melinis repens* was observed to be the most dominant species in the study area. The adaptability of these species to elevated temperatures not only supports their growth but also enhances their competitive advantage in grassland habitats, allowing them to effectively utilize available resources and establish a strong presence in their ecosystems.

Finally, Group 3 featured species associated with drought treatment intensity, such as *Chascanum pinnatifidum, Aristida meridionalis,* and *Pogonarthria fleckii*. The latter implies that these species are sensitive to the impact caused by drought treatments and their allocation patterns can be greatly impacted. For instance, under severe drought conditions, root length and diameter can decline, but species with strong drought adaptations may maintain or even increase root biomass to enhance survival (Sun et al., 2024).

The analyses conducted through hierarchical cluster analysis (HCA) and Canonical Correspondence Analysis (CCA) demonstrated that species composition varies significantly across different drought treatments. Certain species, such as *Pogonarthria fleckii* and *Aristida meridionalis*, are more closely associated with drought conditions, suggesting they possess drought-tolerant or opportunistic traits that enable them to thrive under stress. Conversely, other species like *Aristida congesta* and *Cyperus fulgens* prefer environments with higher moisture levels, indicating a stronger preference for less drought-affected habitats. This distinction highlights the adaptive strategies of various species in response to water availability and the ecological implications of these adaptations in their respective environments.

CHAPTER 6

6. CONCLUSIONS

This study reveals important insights into the biomass allocation strategies of herbaceous species under varying drought conditions. The lack of significant differences between aboveground and belowground biomass allocation across the four drought treatments (0%,20%,40%,60%) supports the isometric theory, indicating that these biomass components maintain a proportional relationship without a clear trade-off during drought stress. The non-significance between vegetative and reproductive biomass allocation highlights the complex responses of herbaceous plants to drought stress, indicating that short-duration droughts may not sufficiently impact growth patterns to produce measurable differences. This underscores the necessity for a deeper understanding of species-specific adaptations and their ecological implications, as effective conservation and management strategies will be crucial in addressing the challenges posed by increasing drought frequency and intensity due to climate change in arid regions.

Environmental factors such as soil moisture and temperature play pivotal roles in shaping biomass allocation patterns. Notably, the study found no correlation between soil moisture content and biomass allocation, implying that herbaceous plants can maintain stable allocation strategies despite varying moisture levels. However, temperature emerged as the strongest predictor of vegetative biomass, while drought treatments significantly influenced reproductive biomass. This indicates that drought can alter microclimates for species, emphasizing the effectiveness of rainout shelters in simulating short-term drought conditions.

Chlorophyll content varied among species under different drought treatments, with certain species like *Aptosimum lineare* and *Ocimum americanum* exhibiting higher chlorophyll levels under severe drought conditions. This ability to enhance chlorophyll b levels suggests these species can better withstand dry conditions by improving photosynthesis efficiency.

The lack of association between herbaceous plant cover and drought treatment highlights the resilience of species in arid savannas. Species like *Aptosimum lineare, Aristida meridionalis, Chascanum pinnatifidum*, and *Eragrostis lehmanniana* maintain cover despite fluctuating water availability. This allocation pattern suggests that greater investment in aboveground structures enhances plant cover, reflecting their ability to optimize growth under challenging environmental conditions like drought.

Analyses using HCA and CCA revealed significant variation in species composition across drought treatments. With species such as *Pogonarthria fleckii* and *Aristida meridionalis* performing better drought conditions, suggesting they possess drought-tolerant or opportunistic traits. In contrast, species such as *Aristida congesta* and *Cyperus fulgens* prefer environments with higher moisture, indicating a preference for less drought-affected habitats. These findings highlight the adaptive strategies of species to water availability and their ecological implications.

Understanding the biomass allocation strategies of herbaceous plants under drought is crucial for effective conservation and management in arid regions. The study emphasizes that while these plants exhibit resilience through stable allocation patterns, their responses to environmental factors are complex and warrant further investigation. As climate change increases the frequency and intensity of droughts, developing tailored conservation strategies will be essential to support these ecosystems' sustainability and biodiversity.

CHAPTER 7

7. RECOMMENDATIONS

Based on the findings of this study, it is recommended to prioritize the usage of drought-tolerant herbaceous species such as *Aptosimum lineare* and *Eragrostis lehmanniana*, which demonstrated stable biomass allocation and higher chlorophyll content under severe drought conditions, indicating their resilience to water stress in restoration projects. These species are valuable for restoration and management efforts aimed at enhancing ecosystem stability in arid regions. Additionally, forage species like *Cenchrus ciliaris* and *Eragrostis lehmanniana* maintained consistent cover and biomass allocation despite drought treatments, suggesting their potential to provide reliable forage during dry periods; thus, their cultivation should be promoted to support sustainable land use.

Given that temperature significantly influenced vegetative biomass and drought treatments impacted reproductive biomass, establishing monitoring programs to track environmental variables such as temperature and soil moisture is essential for anticipating changes in forage availability and guiding adaptive management strategies. Further research is recommended to explore the influence of environmental factors on species allocation patterns, as indicated by the study's results. A more comprehensive investigation should include additional variables such as soil nutrients, humidity, and topographic slopes to enhance our understanding of these dynamics.

Extending the study over a longer period with annual monitoring would help fill existing knowledge gaps and inform future conservation strategies, particularly in arid ecosystems where such research is currently limited. Additionally, focusing on the specific responses of herbaceous species to varying drought conditions and their implications for forage availability would provide critical insights for adaptive management strategies in the context of climate change. The continuous use of rainout shelters in experimental designs is also advised to simulate drought conditions effectively, allowing for a thorough assessment of how different herbaceous species respond to drought. This approach can yield valuable data to guide future management practices and improve our understanding of the resilience and adaptability of these species in changing environments. Moreover, this study recommends future research to focus on capturing the whole rainy season to capture more results and to do the research over an extended period of time.

CHAPTER 8

8. REFERENCES

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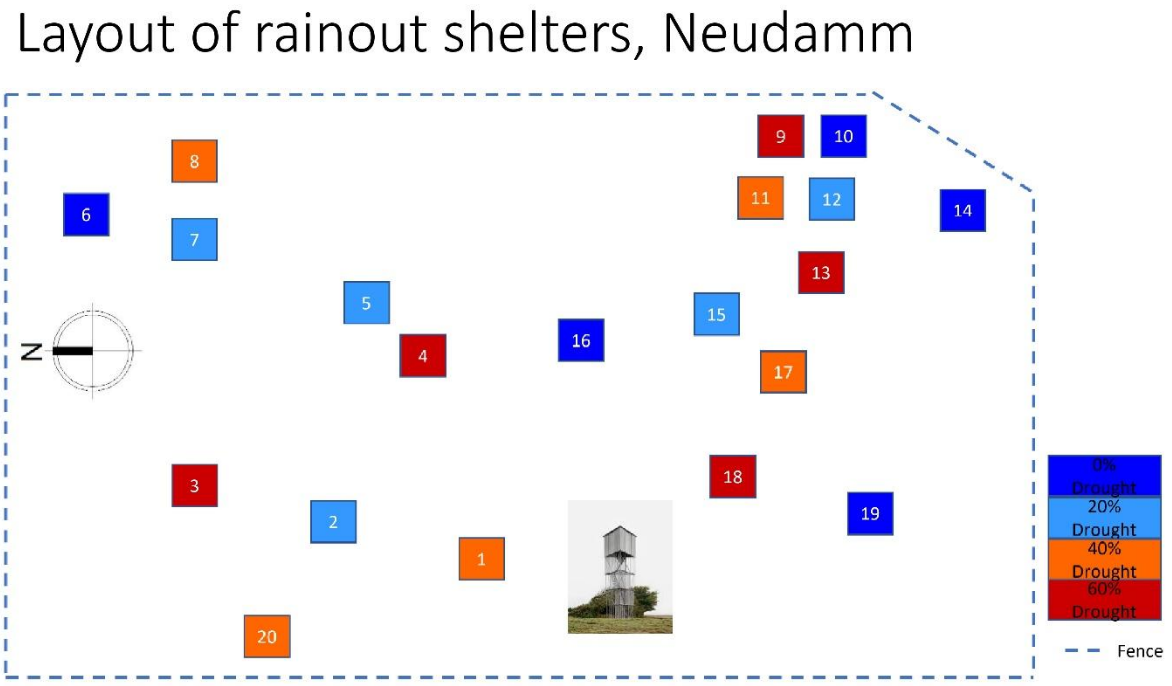
APPENDICES

Appendix 1. Total rainfall per month (mm) for the rainy season at Neudamm Agricultural Farm, central Namibia

Month	Total rainfall per month
Dec-23	8.5
Jan-24	7.5
Feb-24	39
Mar-24	108
Apr-24	7
May-24	0.5
Total	170.5



Appendix 2. Layout of the rainout shelters at Neudamm Experimental farm, central Namibia

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ETHICAL CLEARANCE CERTIFICATE

Ethical Clearance Reference Number: SOS-0192 Date: 31 JANUARY 2024

This Ethical Clearance Certificate is issued by the University of Namibia Ethics Committee (REC) in accordance with the University of Namibia's Research Ethics Policy and Guidelines. Ethical approval is given in respect of undertakings contained in the Research Project outlined below. This Certificate is issued on the recommendations of the ethical evaluation done by the ethics committee.

Title of Project:	VEGETATIVE AND REPRODUCTIVE BIOMASS ALLOCATION RESPONSES OF SELECTED FORB SPECIES TO DROUGHT IN A SEMI-ARID HIGHLAND SAVANNA, CENTRAL NAMIBIA
Student:	MARTHA ETUNA NASHINI
Student Number:	219374932
Supervisor(s):	PROF. EZEKEIL KWEMBEYA DR. FRANSISKA KANGOMBE

Centre for Research Services

Take note of the following:

1. Any significant changes in the conditions or undertakings outlined in the approved Proposal must be communicated to the ethics committee. An application to make amendments may be necessary.
2. Any breaches of ethical undertakings or practices that have an impact on ethical conduct of the research must be reported to the ethics committee.
3. The Principal Researcher must report issues of ethical compliance to the ethics committee (through the Chairperson) at the end of the Project or as may be requested by the ethics committee.
4. The ethics committee retains the right to:

i) Withdraw or amend this Ethical Clearance if any unethical practices (as outlined in the Research Ethics Policy) have been detected or suspected, ii) Request for an ethical compliance report at any point during the course of the research.

The ethics committee wishes you the best in your research.

Dr. Zivayi Chiguvare (Chairperson Ethics Committee)

Prof. Davis Mumbengegwi (Head, Multidisciplinary Res
(Head, Multidisciplinary Research)