# EFFECTS OF SOIL MOISTURE VARIABILITY ON MORPHOLOGICAL AND ANATOMICAL ATTRIBUTES OF ROOTS AND BUDS OF SELECTED RANGELAND GRASSES OF SOUTHERN RANGELANDS OF KENYA

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# DECLARATION AND APPROVAL

I hereby declare that the work contained in this thesis is my original work and has never been submitted for a degree in any other university

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# DEDICATIONS

I dedicate this thesis to my dear parents. First, to my dad, Alexander Kakusu, who has been a role model to me and ensured the successful completion of my education. My mom Veronica Kakusu has been my first teacher and instilled in me the value of hard work and perseverance.

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# TABLE OF CONTENTS

## LIST OF FIGURES

## LIST OF TABLES

## ABBREVIATIONS AND ACRONYMS

| | |
|---|---|
| ASALs | Arid and Semi-Arid Lands |
| FAO | Food and Agriculture Organization |
| GDP | Gross Domestic Product |
| IPCC | Intergovernmental Panel on Climate Change |
| NSC | Non-Structural Carbohydrates |
| SRL | Specific Root Length |
| PRDM | Percent root dry matter |
| RTD | Root Tissue Density |
| SSA | sub-Saharan Africa |

# ABSTRACT

This study evaluated the morphological and anatomical responses of below-ground parts of *Pennisetum mezianum*, *Digitaria macroblephara*,and *Themeda triandra* to moisture variation in the semi-arid rangelands of South Eastern Kenya. Bud and root functional traits, including average root diameter (RD), root tissue density (RTD), specific root length (SRL), percent root dry matter content (PRDM), and non-structural carbohydrates (NSC) were determined.Soil moisture content below the ground surface was monitored to determine its relationship with the aforementioned parameters.

Decline in soil moisture caused significant ($p<0.05$) decrease in bud size, PRDM, and increase in NSC for all three grass species. Generally, RTD increased with increase in soil moisture deficit in all three grass species. For SRL, it significantly increased with a decrease in soil moisture content in *D. macroblephara*. There was no significant variation in the average number of buds and RD, with corresponding variation in soil moisture content.

*Pennisetum mezianum* had significantly ($p<0.05$) higher number of buds, largest bud sizes, largest RD, lowest SRL, lowest RTD, and least amount of NSC content. *Themeda triandra* and *D. macroblephara* had a narrow root diameter, high SRL, high RTD, and a high NSC content. These patterns indicate that the three grass species had developed diverse strategies to withstand water deficit conditions, with *P. mezianum* employing a conservative strategy, while *T. triandra* and *D. macroblephara* employ a timely utilization strategy. Further research should be conducted on more range grass species over multiple seasons to better understand adaptive mechanisms of range grass species to enable us to predict plant community change because of climate change.

# CHAPTER ONE

# INTRODUCTION

## 1.1 Background Information

Arid and semi-arid lands (ASALs) make up to 40% of the world's terrestrial cover, sheltering about a third of the human population and up to 50% of the world's livestock population (McDermott *et al.*, 2010). In Africa, ASALs make up 43% of the land area and host about 40% of the human population, i.e., approximately 268 million people (Cervigni and Morris, 2016). Kenya's ASALs account for about 80% of the land area, supporting over 14 million people and 70% of the country's livestock herd (MacOpiyo *et al.*, 2013).

The main economic activity in the ASALs is livestock production, mainly through pastoralism and agro-pastoralism. Rain-fed and irrigated agriculture and related economic activities are practised in regions that receive higher and more reliable precipitation (Headey *et al.*, 2014). Approximately 40% of Kenya's agricultural Gross Domestic Product (GDP) and 10% of the total GDP is generated from the livestock subsector (Cervigni and Morris, 2016) which, in turn, employs 90% of the ASAL rural population, contributing approximately 95% of the family income (Syomiti *et al.*, 2015).

Erratic rainfall and periodic droughts are common features in ASALs (Irungu *et al.*, 2014; Gikaba *et al.*, 2014) and although pastoralists, since time memorial, have learnt how to cope with these climatic variations, the situation has recently been exacerbated by the global climate change phenomena, whose major parameters include increase in temperatures, reduced and poorly distributed rains coupled with an increase in drought frequency and severity (Gikaba *et al.*, 2014). High ambient temperatures give rise to high evapotranspiration which when it rises above a certain optimum threshold impedes plant water and nutrient uptake and may also damage some plant components.

Soil moisture variation is a critical factor in the ASALs since it affects both plant growth and productivity (Zhang *et al*., 2018). In a typical ASAL, it swings from very high amount during the wet season, to very low during the dry season. Consequently, range plants have over time developed elaborate survival mechanisms to cope with these conditions (Ott *et al.*, 2019). For example, roots of range grasses promptly respond to variation in soil moisture and temperature by adjusting their form, physiology, and structure to compensate for alterations in the availability of these resources. Successful growth and development of below-ground buds, which ensure successive tiller production, compensation for annual tiller mortality, and hence the perpetuation of range grasses is important grass husbandry practice. Growth and morphogenesis of grasses follow a clonal growth pattern whose processes are mainly localised around the root crown meristems and in the auxiliary region where continuous cell enlargement, occasional cell division, and cell differentiation occur (Romberger, 1963). Initially, the parent tillers develop from the tiller apical meristem; subsequently, axillary buds on parent tillers develop into new tillers (Dahl, 1995). These buds are essential as they are the source of meristematic tissue, which contributes to the plant community's response to moisture variations in ASALs.

Another important aspect of grassland ecology is longevity, which is primarily influenced by the proportion of stem bases with active axillary buds within each grass-root crown. Re-growth largely depends on activation and subsequent outgrowth of buds when a large proportion of above-ground tissue is removed. Non-structural carbohydrates (NSC) reserves are used during periods of moisture deficiency for re-growth and survival by supplying energy to axillary buds to initiate new growth or support ongoing growth, which eventually contributes to new tiller development (Wu *et al*., 2021). Root carbohydrate reserves cushion grasses against the effect of fire, herbivory, drought, or any other disturbance. Plants with sufficient reserves are more likely to support bumper growth after disturbance (Pembleton *et al*., 2010). Under moisture deficit, the respiration of storage organs is sustained by NSC until that time when soil moisture rises to the required level, and the plant resumes photosynthesis and carbohydrate supply to the other parts of the plant, including roots and root crown (Pembleton *et al*., 2010). Grass roots, crowns, and buds are closely intertwined, and one cannot function without the other. Below-ground buds utilize NSC from the root and crown to form tillers which are sustained by the NSC until the point where they can produce their own photosynthates. Production of these photosynthates is made possible by nutrients in the soil and moisture absorbed by the root system. As these tillers mature, a new cohort of buds is formed, and NSC builds up in anticipation of the next season's growth, with the process repeating itself all over again. It is from this process that previously bare ground is rapidly covered by grass a few days after the onset of rainfall. Understanding the effect of soil moisture variability on root and bud morphology as well as anatomy, including the bud bank, NSC reserves, and their development, against the backdrop of cyclic patterns of utilization and re-establishment of root and shoot biomass is paramount, considering the production and persistence of perennial grasses in the plant community.

## 1.2 Problem statement and justification

Many rangeland ecosystems in eastern Africa are projected to get drier, while the timing and amount of precipitation are expected to shift (Intergovernmental Panel on Climate Change, (IPCC, 2015). In the recent past, the severity and frequency of droughts have significantly increased (Cervigni and Morris, 2016), resulting in decreased vegetative productivity in rangelands. These changes have had negative impacts on grasslands, a key natural resource that supports pastoral livelihoods. Plants exposed to an extended drought period exhibit subdued production, and their growth is limited (Zhang *et al.*, 2018). Globally moisture deficit is one of the main abiotic factors limiting pasture production (Pejman *et al.*, 2019). For instance, in perennial grasses of ASALs, when the soil moisture conditions ideal for active plant growth are not met, axillary bud production, viability, and activation usually are adversely affected and limit the re-growth potential of range grass species. Consequently, there is a reduction in stand longevity and increased deterioration of rangelands. Range grasses, however, have over the years developed adaptive mechanisms that enable them to produce new tillers replacing any that might have been lost through any range use activities, the main one being overgrazing.

In instances where tiller recruitment is inhibited by moisture deficit, new tiller growth can be initiated through belowground axillary buds that have survived the moisture deficit or from buds that develop after the moisture deficit. The number of axillary buds on the root crown of a given grass species (also known as bud bank) plays an integral role in a pasture's structure, its productivity, and resilience. The ability of range grasses to withstand environmental stress is a function of the size of their bud banks (Russell *et al*., 2013). Bud banks, on the other hand, depend on new buds, the longevity of present buds, and the general bud dynamics (Ott and Hartnett, 2011). Therefore, grasses with an extensive belowground bud bank and extensive root system can easily recover after a disturbance.

The capacity of any grass to withstand moisture deficit is a function of the size of its bud bank, the longevity of existing buds, and the general bud dynamics. However, little is known about the effects of moisture deficit on axillary bud banks of the common range grass species of east Africa. Studies on the significance of tissue structure have largely been restricted to above-ground organs, a bias largely attributed to the fact that above-ground parts are easier to study than the below-ground ones. With the impact of the currently unfolding climate change phenomenon, there is an urgent need for plant and rangeland scientists to have a thorough understanding of how the root systems of grasses respond to never-ending fluctuations in soil moisture content (Eshel and Beeckman, 2013).

There has been a substantial scarcity of comprehensive assessments of below-ground parts' morphological and anatomical responses to moisture deficit. In sub-Saharan Africa (SSA), studies on root crown axillary buds have been few, leaving a big knowledge gap on morphological and anatomical patterns of bud development, which is crucial in predicting plant community changes as a result of external disturbance. Likewise, studies on the effect of moisture deficit on root morphology have been scarce with several of them reporting an increase in root growth with increase in moisture deficit (Perlikowski *et al*., 2019**;** Guo *et al*., 2020; Zhang *et al*., 2018). The theory behind the increase in root growth is that roots extend deeper in the soil profile in search of water due to moisture deficit. Other studies have reported a decrease in root elongation with increase in moisture deficit (de Vries *et* *al.*, 2016), which is attributed to increase in soil impedance due to decreased soil water potential and because root elongation is a hydration process.

This study, therefore, sought to increase understanding of the mechanism behind grass species survival and specifically the morphological and anatomical changes of below-ground parts of grasses in response to soil moisture variation. A better understanding of bud bank dynamics will deepen appreciation of the relationship between the formation and maintenance of below-ground meristems, which will, in turn, establish a scientific basis for efficient management of range grass species against the backdrop of the current and future impacts of climatic variability and/or climate change. Finally, this study's findings will inform the formulation of management strategies to ensure the sustainable productivity of forage in the ASALs.

## 1.3 Broad objective

The broad objective of this study was to determine the effects of soil moisture variability on morphological and anatomical parameters of roots and buds of selected grasses native to southern rangelands of Kenya.

## 1.4 Specific Objectives

1. To determine the effects of soil moisture variation on axillary bud numbers and sizes of *P. mezianum, T. triandra,* and *D. macroblephara*.
2. To evaluate the effect of soil moisture variation on root tissue density, specific root length, root diameter, and root dry matter content of *P. mezianum, T. triandra,* and *D. macroblephara*.
3. To assess the effect of soil moisture variation on NSC content in root crowns of *P. mezianum, T. triandra,* and *D. macroblephara*.

## 1.5 Research hypotheses

This study attempted to answer the following questions:

1. How does soil moisture variation affect the dynamics of root crown axillary buds in *P. mezianum, T. triandra, and D. macroblephara*?
2. How does soil moisture variation affect the anatomical and physiological parameters of *P. mezianum, T. triandra, and D. macroblephara*?
3. How does soil moisture variation affect the carbohydrate reserve levels of *P. mezianum, T. triandra,* and *D. macroblephara*?

# CHAPTER TWO

# LITERATURE REVIEW

## 2.1 Introduction

Grasslands make up to 35% of the total land cover in the world (Food and Agriculture Organization, FAO, 2019). The productivity of these lands varies with time and space. It highly depends on rainfall, with grasses being the dominant contributors of primary production and largely influencing the frequency of fire, herbivory, and all human activities (FAO, 2019).

Grasses flourish under varied conditions because of their immense adaptability. They number up to 770 genera and about 12,000 species, making them one of the most treasured and largest groups of flowering plants (Kellogg, 2015). After Compositae and Orchidaceae, grasses have the highest number of genera and the fifth-highest number of species after Orchidaceae, Rubiaceae, Compositae, and Leguminosae (Hodkinson and Parnell, 2007).

The climax vegetation types of the steppes of Asia, North American tallgrass prairie, and the African savannas are made of grasses. Among the herbs, grasses are the most dominant species across tropical savannas. Its importance as a source of forage for livestock and other herbivores; and cereals for human beings cannot be overemphasised (Hodkinson, 2018). Apart from being a food source, grasses also play a crucial role in global carbon cycles and thus regulate greenhouse gases. They also play a big role in desertification and climate change mitigation, as well as biodiversity conservation.

Range grasses are continuously exposed to several abiotic and biotic factors that affect food availability for both humans and animals. Land-use changes in the grasslands have led to vast lands being converted into croplands. Likewise, overgrazing, caused by overstocking, has contributed to the degradation of grasslands (Dubois, 2011). Abiotic factors include extreme temperatures, moisture deficit, and salinity, which are detrimental to plant growth and development (Shakeel *et al.*, 2011). Climate change is projected to cause a decrease in rainfall and increase in temperature, leading to increased drought frequency and decreased rainfall amounts for many rangelands of East Africa. These changes are projected to cause a myriad of negative effects on the range ecosystems. Over the years, grasses have shown high adaptability to these stresses and have flourished despite the many constraints. Expected shifts in climate over the next 50 years will probably affect nutrient, hydrological and energy cycling, in rangelands. For this reason, further research that improves our understanding of how climate affects rangeland grasses is urgently needed to enable us to make long-term predictions of plant and ecosystem responses to global change and to influence management.

## 2.2 Importance of grasses to Livestock production

***"All flesh is grass!"***This widely-quoted verse in the Old Testament (Isaiah 40:6) is literally true when we think of livestock production. Herbivores harvest and ingest forage (sometimes dry and dirty stuff) and within hours convert it into meat or milk–man's delicacies. How this unique category of animals accomplishes this very critical food-chain process is, to date, a big mystery to the best animal nutritionist and physiologists. Herbaceous plants, and in particular grasses and forbs 'drive' this process by providing forage—the raw materials of meat and milk production. Suffice it to say that without grasses, there is no livestock and without livestock, there is no meat or milk—a dire strait. As mentioned earlier, livestock production is an important economic activity in the ASALs, even though these areas experience a wide array of challenges, especially those related to climate variability and/or change. To sustain livestock production worldwide, a thorough understanding of the growth and development of the grass is critical. This is particularly so in the ASALs, where a wide range of untoward environmental factors act simultaneously on the plants throughout the year, restricting their growth and development. In Kenya, despite the high potential of the ASALs to produce meat and milk, there is still a huge deficit. The country normally relies on imports from neighbouring countries such as Tanzania, Somalia, Sudan, and Ethiopia (Kirwa, 2019). The low livestock productivity in the country can be explained by inadequate feed in terms of both quantity and quality (Koech *et al*., 2016), which are influenced by the phenological stage of plant growth, harvesting frequencies, grass species, and climatic conditions (Bumb *et al*., 2016).

Pasture availability has been low and declining in Kenya's ASALs because of factors such as land fragmentation, increase in livestock numbers, human population, and droughts. In addition, food insecurity and famines have been rampant since the 1990s in the ASALs of Kenya (Amwata, 2013). This has increased pressure on the ASALs to increase livestock numbers leading to overgrazing and loss of palatable perennial grass species that have been replaced with annuals and invasive species.

## 2.3 Impact of soil moisture variation on grass growth

Among the many environmental stressors of grasses, soil moisture variation is the most important, especially its deficit whose frequency is projected to increase in many regions of the earth with increase in climate change grip (Zheng *et al*., 2017; Shukla *et al*., 2019). Droughts (prolonged dry periods within the natural climate cycles) are expected to cause a myriad of adverse effects on range grasses and major shifts in key grassland biomes of the world. Although droughts are a common occurrence in ASALs, an increase in their frequency can adversely affect range productivity. As mentioned earlier, range plants have over the years developed adaptive mechanisms that have enabled them to flourish despite the effects of droughts through physiological and morphological adaptations. However, recurrent droughts may lead to increased moisture deficit and plant mortality, despite this adaptation.

Plants experience moisture deficit when available moisture in the root zone cannot sustain growth or when transpiration rates are too high (Shakeel *et al.*, 2011). Susceptibility of range grasses to moisture deficit depends on the severity of moisture deficit, the grass species, developmental stage, and presence of other accompanying stress factors (Demirevska *et al.*, 2009). With an increase in moisture deficit, mortality is enhanced in plants as they are susceptible to hydraulic failure and carbon starvation because of stomatal closure for water conservation (McDowell *et al.*, 2008). In addition, dominant native species are likely to be affected, leading to decreased numbers. Consequently, the plant community's susceptibility to invasive species may increase.

Moisture deficit further affects cell membrane integrity, osmotic water relation, water integrity, and turgor pressure (Praba *et al.*, 2009). As a result, cell growth and development are inhibited, making it the most sensitive physiological process (Shakeel *et al.*, 2011). Moreover, increased water deficits lead to decreased enzyme activity, a decline in energy sources, and water inhibition leading to decreased germination rates and plant establishment (Taiz and Zeiger, 2010), eventually affecting yields, plant physiology, and growth (Tawaha *et al.*, 2017).

Moisture deficit affects not only the cellular activities of grasses (Staniak and Kocoń, 2015) but also plant height, leaf, and root growth (Kamau, 2020). Koech *et al.* (2016) reported that with increased moisture deficit in plants, there is decreased shoot development and the number of shoots per plant. Furthermore, moisture deficit leads to a decreased rate of shoot growth, affecting the plant's ability to sustain sufficient plant water balance (Pembleton *et al.*, 2009). Additionally, increased moisture deficit leads to decreased leaf area, early leaf senescence, and limited photosynthesis (Pembleton *et al*., 2009). The overall effect is a reduction in above-ground biomass production.

Moisture deficit has detrimental impacts on both reproductive and vegetative stages of grasses, with the latter being more adversely affected (Tawaha *et al*., 2017). Moisture deficit has also been shown to cause a decrease in the number of grains per spike in barley (Samarah *et al*., 2009). Generally, there is a decline in plant height, grain yield, and biological yield in plants experiencing moisture deficit (Nezami *et al*., 2008). Adaptive changes in grasses include changes in osmotic potential, growth rate, morphology, and physiology of the plant, which enable grasses to acclimatize to moisture deficit (Demirevska *et al*., 2009).

## 2.4 Role of axillary bud banks in perennial grass species

Until recently, the focus in grass stand dynamics has been mainly on seed banks, with axillary buds receiving little or no attention. Yet, Bud banks play a crucial role in grass growth. Harper (1997), whose work mainly focused on the dynamics of seed banks and seed production, coined the term “bud bank”. Harper referred to “bud and seed banks” metaphorically as the hidden ‘wealth’ of dormant plants. Buds and seeds are morphologically, anatomically, physiologically, and functionally different plant organs. Seeds are produced via sexual recombination, while buds are produced clonally from a single genet. Buds are normally attached to the parent plant, while mature seeds are harvested and independent of parent plants (Harper, 1997).

Bud banks include apical, adventitious, accessory, and axillary buds. Determinants of bud bank size are the rate of inputs (bud natality) and outputs (outgrowth, mortality), and bud activity. Bud natality can be seasonal or continuous as it is influenced by weather and/or triggered by disturbance. Development usually occurs during plant ontogeny, and bud activity (dormant or active buds) determines the effects of bud bank size on above-ground population dynamics (Ott *et al*., 2019).

Bud formation coincides with a period of bud dormancy whose length depends on the individual plant or the surrounding environmental condition. Therefore, the number of buds that remain dormant at the onset of growth plays a crucial role in bud dynamics and overall above-ground plant population dynamics. For example, a high number of active buds results in high rates of tiller recruitment during subsequent periods of active growth. The downside of it, however, is that during a period of unfavourable conditions, there are few buds that can withstand the stress, and therefore, reduce the regenerative capacity of the grasses when the disturbance is removed (Shefferson *et al.*, 2014; Ott *et al*., 2019). Therefore, it is expected that resilient and persistent perennial grasses can maintain a bigger bud bank, resulting in a more stabilised population when the conditions are not favourable and population recovery when conditions are favourable.

Despite the high adaptability of range grass species to seasonal change in moisture availability, climate change is expected to substantially alter the bud bank dynamics, and more so with the increasing drought frequencies. Soil moisture deficit interferes with axillary bud viability and/or activation and inhibits the development of new green buds on root crowns, and consequently affects the regrowth potential of a plant species (Pembleton *et al.*, 2010). Generally, there is a decrease in bud numbers per shoot or a reduced number of shoots per plant with an increase in moisture deficit (Reichmann *et al.*, 2013). The overall effects include reduction in stand longevity and ultimately degradation of rangelands.

## 2.5 Effect of soil moisture variations on axillary bud bank dynamics

Grass species that are well adapted to extreme soil moisture deficits have been reported to have a high number of buds. Large bud banks enable grasses to produce more tillers as they can utilize more resources when they are abundant and act as buffers when resources are limited. However, this is not solely the case as some other factors like seed bank generation and bud longevity might be more important (Dalgleish *et al*., 2012).

Previous studies on bud numbers in sub-Saharan Africa (SSA) suggest more reliance on seed production than vegetative reproduction (Hartnett *et al.*, 2006). This is in contrast to the prairies of North America, South America, Europe, and Asia,where more than 99% of new growth comes from below-ground buds (Benson and Hartnett, 2006). However, it is important to note that such studies are scarce in SSA, and the few available have been conducted in a small area and with a limited number of grass species. Additionally, there have been conflicting results on the effect of soil moisture deficit on bud numbers and sizes. For example, VanderWeide and Hartnett. (2015) reported a steady increase in the number of buds during a two-year drought on the tallgrass prairie. Contrasting results were reported by Qian *et al*. (2017), who observed that bud numbers decreased with increased moisture deficit in the temperate Steppes of northern China.

Bud sizes vary among grass species. Large buds are associated with more developed and active vascular connectivity with the polar auxin transport system (PATS) and an increase in nutrient import into the bud (Waldie *et al*., 2010). Large buds store more resources and thus increase the possibility of them developing to new tillers. Furthermore, they have higher bud longevity and large bud banks comprising multiple-year cohorts of buds (Ott *et al*., 2019). Studies on the effect of moisture deficit on bud size are few. Pembleton *et al*. (2010) reported a decrease in bud size when there is a severe water deficit.

## 2.6 Effect of soil moisture variations on grass roots

Growth by cell expansion heavily depends on the water supply to the cells and is a key factor in the multiplication of cells. Therefore, moisture deficits affect the overall growth and development of plant parts, with leaves being more affected than roots. The reduction of soil water potential leads to a slow osmotic change in leaves. When this happens, the cell wall loosening ability either decreases or does not increase substantially, resulting in growth inhibition. However, in the root system, roots continue to grow under reduced levels of soil water potential. Reduction in water potential in roots results in partial turgor pressure and water potential gradient re-establishment. In the process, there is a fast reduction in turgor pressure that leads to an increase in the loosening of the cell (Xu and Liu-Kang, 2000). Thus, with increased moisture deficit in plants, the root: shoot ratio is expected to increase (Wu and Cosgrove, 2000).

During the initial phases of moisture deficit, plants adapt by maintaining a high rate of photosynthesis in the leaves. However, during an extended period of water deficit, the morphological and physiological adjustments of roots are crucial in adapting to changes in the environment (Farooq *et al*., 2009). For example, with a decrease in water deficit, shoot growth decreases in a similar proportion (Guo *et al*., 2020).

Perennial C4 grasses have been shown to have extensive deep root systems, with a root biomass of about 14 Mg ha$^{-1}$ (Jackson *et al*., 1996). Grasses with a deeper root system can utilize water resources found in deeper soil profiles and hence are better adapted to water deficiency (Koech *et al*., 2015). In addition, grasses maintain a high root: shoot ratio even after drought has ceased, enhancing persistence and/or stimulating subsequent growth (Zhang *et al*., 2016).

Many studies have shown that root structure, length, and distribution are the key factors for extracting moisture from the soil during the growing season (Farooq *et al*., 2009). An extensive root system allows plants to absorb water from upper soil profiles that would otherwise be lost by evaporation and supports plant development during the early phase of growth (Shakeel *et al*., 2011). In addition, fine roots are responsible for acquiring water and nutrients when scarce, while heavier roots penetrate the soil profile more and absorb more water during periods of high availability (Pérez-Harguindeguy *et al.*, 2013). Other important functions of dense root systems include transport of water to above-ground parts, anchorage to the soil, space occupancy, support for fine root replacement in the soil, and storage of NSC(Klimešová *et al*., 2018; Pausas *et al*., 2018).

## 2.7 Relationship between NSC storage and soil moisture variations

Photosynthesis is the process through which plants, algae, and certain bacteria turn sunlight, carbon dioxide (CO2), and water into food (sugars also known as non-structural carbohydrates{NSC}) and oxygen. NSC are the main products of photosynthesis and are, in turn, the main substrates for plant respiration (Wiley *et al*., 2013). They play an important role in regulating the key physiological activities of plants, including buffering of plants from adverse environmental conditions (Ji *et al*., 2020). Major physiological activities of plants include nutrient absorption, respiration, organic secretion, and plant growth. In addition, NSC plays a vital role in plant defence, mechanisms including delaying or preventing plant death and/or drought resistance (Ji *et al*., 2020).

NSC includes soluble sugars such as glucose, fructose, and sucrose, as well as starch and fructans. Starch is the major storage constituent of grasses and also acts as a buffer for drought-instigated disparities that occur during resource acquisition by photosynthesis and carbon-sink activities (Muller *et al*., 2011). However, starch is less labile than soluble sugars, which can easily be broken down to release simple sugars used for growth (Priyadarshini *et al*., 2016). In addition, soluble sugars take part in other physiological functions such as maintenance of cell turgor and osmotic potential, defense, signaling, respiration (Nardini *et al*., 2016), and recovery process after a disturbance has been removed (Guo *et al*., 2020). Sucrose is the dominant NSC in C4 grasses and has been shown to enhance fast above-ground growth at the onset of wet seasons (Souza *et al*., 2010).

Grasses adapt to moisture deficit by translocating carbohydrates from above-ground growth to their root system (McNaughton *et al*., 1998). Studies have shown that root reserves will increase with increased moisture deficit as roots are the primary storage organs and nutrient acquiring (Craine, 2006; Snyman, 2009). For example, in a study on *T. triandra*, root reserves increased by up to 20% when moisture deficit was increased by 25% (Oosthuizen and Snyman, 2003). Maximum root reserves are expected at the peak of the dry seasons (Danckwerts and Gordon, 1990; McNaughton *et al*., 1998). In their work, Pembleton *et al*. (2009) reported that for plants experiencing moisture deficit, there was an increase in soluble sugars in the root system despite the decrease in photosynthesis activity and even after the death of above-ground growth. Plants exposed to moisture deficit have been shown to have higher soluble sugar concentration and vegetative storage proteins inside the root system (Erice *et al*., 2007).

# CHAPTER THREE

# MATERIALS AND METHODS

## 3.1 Study area

The study was conducted at Kajiado Demonstration Farm in Dalalekutuk Ward, Kajiado County, Kenya. The farm is approximately 70 km south of Nairobi City, along Nairobi-Namanga Highway (Figure 3.1), and is approximately 365 ha, 1000 m above sea level and within latitudes 1°48′ S and 1°50′S, and longitude 36°47′E and 36°48′E.

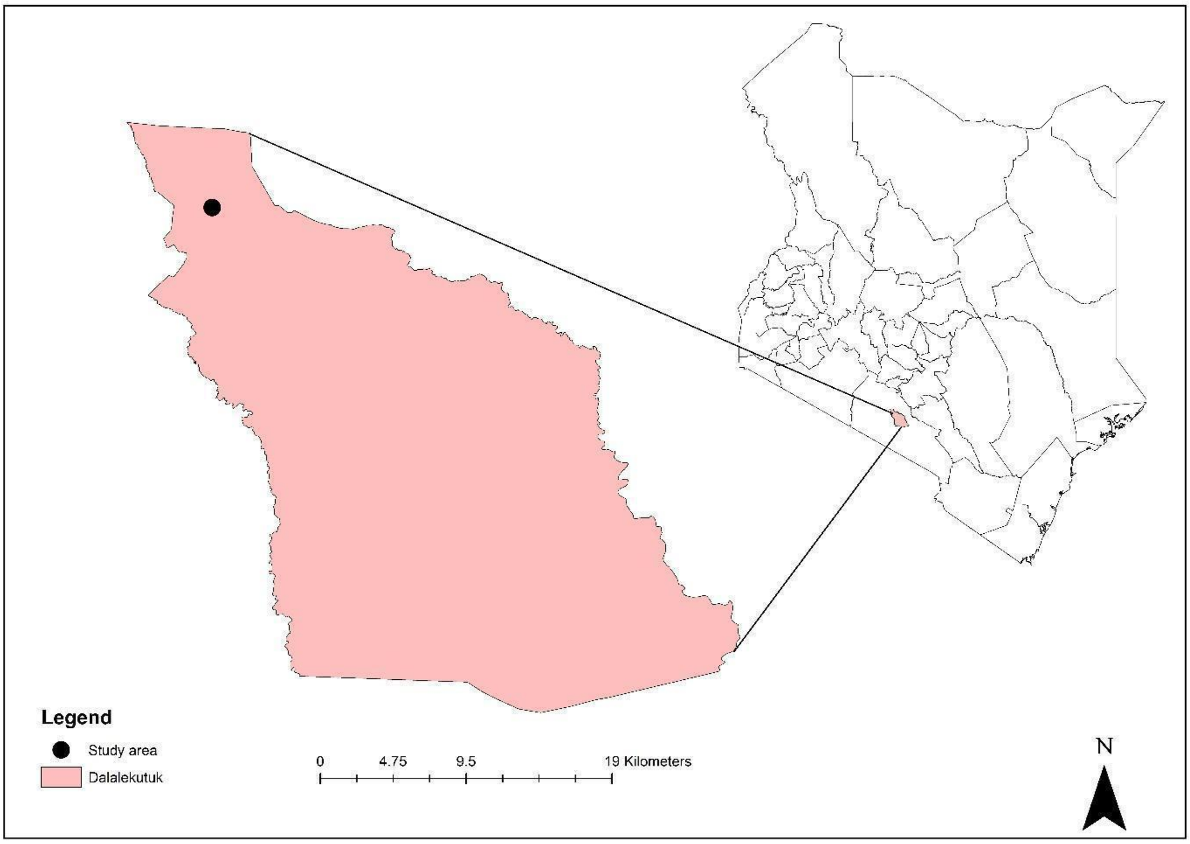


**Figure 3. 1. Map showing Dalalekutuk ward in Kajiado County in relation to Kenya**

The area experiences a bimodal rainfall pattern, with long rains falling between March and May and short rains falling between October and December. The area experiences a dry spell between January and March and June to October, with the latter being more prolonged than the former (Gikaba *et al*., 2014). The farm is characterized by poorly drained black cotton soils (vertisols), which have a high clay content and a high level of calcium carbonate and hence an impeded drainage. The natural vegetation of the study area is savannah grassland, dominated by *P. mezianum, T. triandra, D. macroblephara* grasslands,and *Acacia* trees. Our study focused on these three grass species.

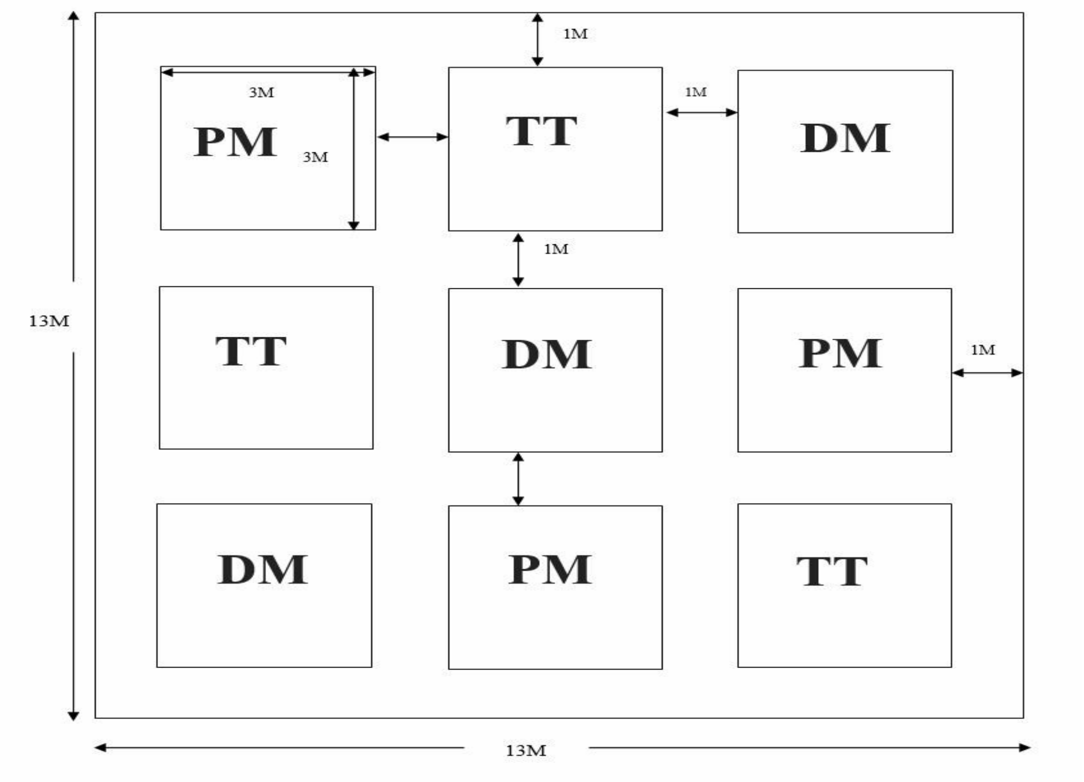
*D. macroblephara* is a perennial stoloniferous bunchgrass forming open tufts from a knotty rootstock that grows up to 100cm high. The grass is common in soils with clay and is primarily found in ecological zone IV and V and rocky areas. The grass is dominant in northeast Africa and east Africa and is a relatively palatable species.

*P. mezianum* is a perennial tufted grass with a short stout woody rhizome that grows up to 120cm. The grass has moderate grazing value, can resist excess grazing pressure, and is commonly found in poorly drained soils. This grass is avoided by grazing animals when senescent or mature because of its wiry or woody structure and low palatability (Odadi *et al.*, 2013).

*T. triandra*, on the other hand, is a perennial tussock with erect culms that extend up to 200cm highand is widespread in the rangeland ecosystem of Africa, Asia, and Australia. It has a high grazing value and is fire resistant. The grass is common in various soil types and is mainly found in ecological zones III, IV, and rarely in V and VI. *T. triandra* is more susceptible to grazing.

### 3.2 Experimental design and layout

The experiment was a completely randomized, two-way factorial design comprising three grass species (*P. mezianum, T. triandra,* and *D. macroblephara)* and five sampling dates spaced at approximately 2-week intervals between January and March 2021. A 13×13m main plot was identified within the farm and fenced off. The plot was cleared of all vegetation, ploughed, and harrowed to a fine tilth. The plot was then subdivided into nine subplots measuring 3×3 m with a 1m buffer strip around each subplot (Figure 3.2 below). The three grass species were randomly allocated to the nine contiguous sub-plots resulting in three sub-plots per grass species.



PM= *Pennisetum mezianum*, TT= *Themeda triandra*, DM= *Digitaria macroblephara*

**Figure 3. 2.Layout of experimental plot**

Each grass species was established in its sub-plots from tuft splits obtained from the already established plants within the farm. Routine husbandry practices such as the application of manure and fertilizer at planting, watering, and weeding were applied uniformly across all the study subplots until all the grasses were well established (to flowering stage) in all the subplots.

### 3.3 Data collection

This mainly entailed tracking the soil moisture content during the study period, determining the number and size of buds around the root crown; measuring the root diameter, and root length; calculating root tissue density, specific root length, and percent root dry matter as well as estimating NSC content during the study period. The methods used to determine each of these parameters are described in detail in the sections below:

#### 3.3.1 Determination of soil moisture content

Soil moisture content was determined by gravimetric method (Russel, 1950). A soil sample from a random point within the 3×3m subplot was obtained using a hand auger driven down to 15 cm depth. The sample was immediately weighed and placed in a can which was tightly closed and transported to the university laboratory for drying. The samples were dried at 110 $^{o}$C for 24 hours. Percent moisture content was calculated using the formula below:

$MC = (FW - DW)/DW \times 100$

Where:

MC = moisture content

FW = fresh weight

DW = dry weight

#### 3.3.2 Determination of root crown bud numbers, bud sizes and average tiller height

On each sampling day, an individual plant (genet) was randomly selected from each of the three subplots allocated to each grass species, it was excavated, and placed on a wire mesh screen (1mm) for root washing. The root systems of each plant were then washed thoroughly with running water from a hose pipe to remove all the soil, then placed in plastic bags and stored in a cooler box. The samples were later transported to the university laboratory for further analysis.To determine the average number of buds and their sizes, three tillers from each genet were randomly selected, with the sheaths carefully removed and the tiller placed under a dissecting microscope to make the counting of the buds easier. Only the viable (turgid) buds were counted. Basal bud widths were also determined and used as proxies for bud sizes. The basal width was measured by means of a vernier caliper with an accuracy of 0.01mm. Tiller heights were measured from the base to the tip of the longest leaf.

### 3.3.3 Determination of root parameters

All excavated plant genets were separated into above-ground and belowground biomass by clipping them at the culm base. A scanner attached to a PC was used to collect images of the roots from which the root parameters (root diameter, total root length, and volume) were estimated using the Image j software. The root materials were then oven-dried at 72ºC for 72 hours, and dry weight determined. From these primary data, root tissue density (RTD) was calculated by dividing the total root dry weight by the root volume (g/cm$^3$). On the other hand, specific root length (SRL) was calculated by dividing total root length by the total root dry weight (m/g), while percent root dry matter content (PRDM) was calculated by dividing total root dry weight by total root fresh weight.

### 3.3.4 Determination of NSC

NSC comprises all soluble sugars (TSS) and starch, which were determined by the Anthrone Method (Yemm *et al.*, 1954). Dry root materials were ground using a ball mill fitted with a 1mm screen. Approximately 30 mg of ground root materials were placed into a 10ml screw-cap micro-centrifuge tube, then 1.5 ml of 80% ethanol was added. The mixture was stirred and incubated at 90º C for 10 minutes in a shaking water bath and centrifuged at 13000 rpm for 1 minute to extract the ethanol-soluble sugars. This process was repeated two times to ensure all the sugars were extracted. The three supernatants were retained for TSS determination.

The supernatants from the soluble sugar extraction were used to estimate the starch content of the root material. First, the residue was boiled in 2 ml distilled water for 15 minutes, and allowed to cool down to room temperature. Then, 2 ml 9.2 M (perchloric acid) $HClO_4$ was added, and the mixture was shaken for 15 minutes. Then, 4 ml distilled water was added, and the mixture centrifuged at 4000 rpm for 5 minutes. A further extraction was carried out with 2 ml 4.6 M $HClO_4$. The two supernatants were combined for starch determination.

Sugar and starch contents were estimated by means of mass spectrophotometer at 625 nm (Yemm *et al.*, 1954). Sugar content was estimated using the regression equations based on the standard glucose solutions and starch concentration by multiplying the glucose concentration by a conversion factor of 0.9 (Osaki *et al.*, 1991).

### 3.4 Data analysis

All analyses were conducted using the R statistical software. To test whether grass species and sampling dates had a significant effect on bud numbers and sizes, root parameters and tiller height, and NSC, a two-way analysis of variance (ANOVA) at 95% confidence level was conducted. Tukey’s HSD post hoc was used to differentiate the means. Pearson correlation coefficient was calculated to identify correlation among the root morphological parameters, below-ground bud parameters, between root parameters and NSC, and between below-ground buds and NSC.

# CHAPTER FOUR

# RESULTS AND DISCUSSION

## 4.1 Results

### 4.1.1 Soil moisture content across the sampling dates

The highest soil moisture contents were recorded on the first sampling date (33.6%) which was done just after the conclusion of the short rains (Figure 4.1), and the third sampling date (42.1%) which was done when there was erratic rainfall during data collection period. The lowest soil moisture content (14.8%) was recorded on the fifth sampling date.

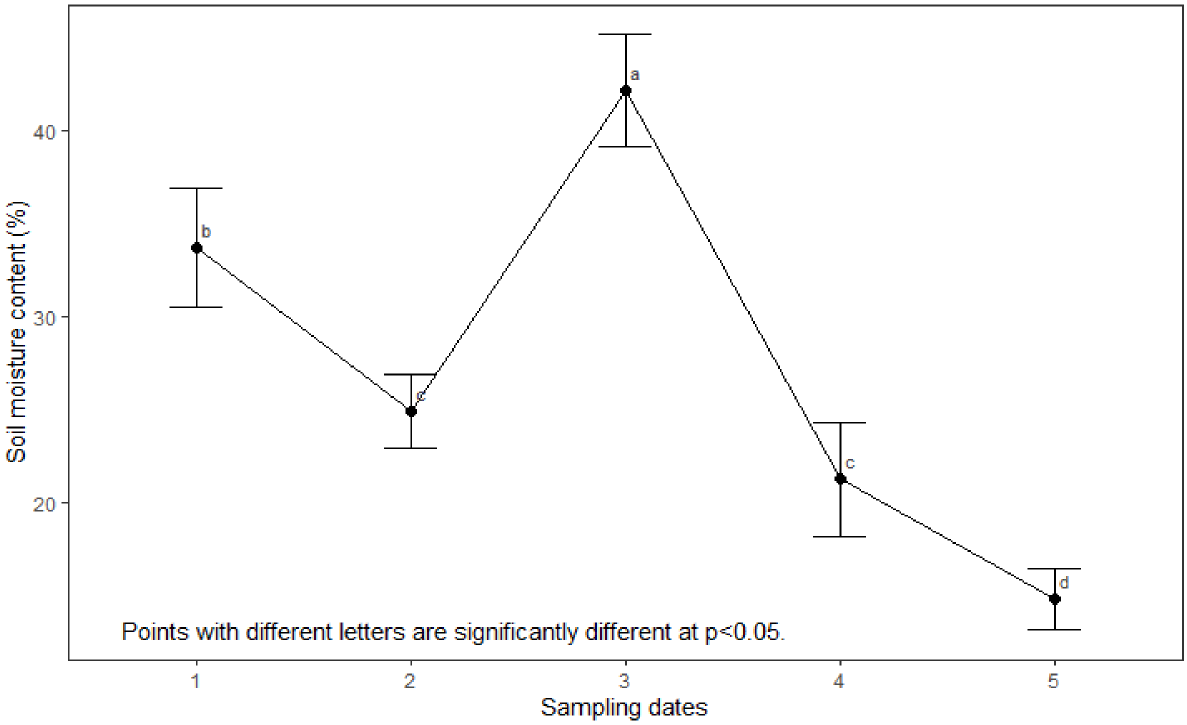


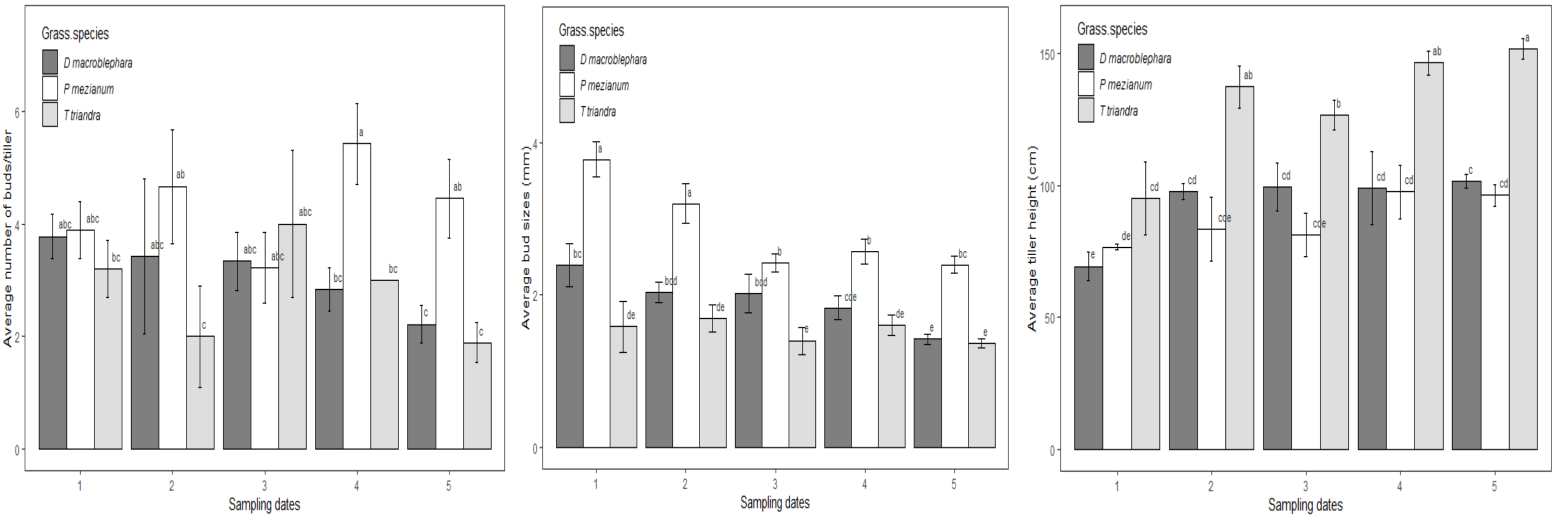
**Figure 4. 1.Mean soil moisture content (%) across five sampling dates**

### 4.1.2 Effects of soil moisture variability on the average number of buds per tiller, bud sizes, and tiller height

Figure 4.2 presents the average number of buds per tiller, average bud sizes, and average tiller heights across the three grass species at different soil moisture levels. Among the three grass species, *P. mezianum* had significantly ($p<0.05$) higher number of buds (4.3) per tiller (Figure 4.2a) than the other two species; *D. macroblephara* and *T. triandra* were not significantly different (3.1 and 2.8, respectively). The effect of soil moisture variability on the number of buds per tiller was not significant ($p>0.05$). *P. mezianum* had the lowest number of buds on the first and the third sampling dates, while *T. triandra* had the highest number of buds on the same sampling dates, which coincided with the highest soil moisture content.

Bud sizes varied significantly ($p< 0.05$) across the grass species and soil moisture content levels. On average, *P. mezianum* had the largest bud size across all sampling dates (Figure 4.2b), while *T. triandra* had the smallest. Bud sizes decreased significantly ($p<0.05$) with decrease in soil moisture content in *D. macroblephara* and *P. mezianum*.

Average tiller heights were significantly ($p<0.05$) different across the grass species and different soil moisture levels. Of the three grass species, *T. triandra* was significantly ($p<0.05$) taller than the other two and across all the sampling dates (Figure 4.2b).



a) b) c)

**Figure 4. 2. Average number of buds per tiller, average bud sizes, and average tiller height (cm) of the three grass species at different soil moisture contents**

*Bars with different letters are significantly different at $p<0.05$.*

### 4.1.3 Effects of soil moisture variability on root diameter (mm), root tissue density (g cm$^{-3}$), specific root length (m g$^{-1}$), and root dry matter (%)

Table 4.1 represents RD (mm), RTD (g cm$^{-3}$), SRL (m g$^{-1}$), and PRDM for the three grass species in relation to changes in soil moisture content. Soil moisture variation had a significant effect ($p<0.05$) on RD, with *P. mezianum* having the highest RD across all soil moisture levels. The highest RD (1.44mm) was recordedon the second sampling date but *T. triandra* consistently had a higher RD than *D. macroblephara*. Apparently, soil moisture variability did not significantly affect ($p>0.05$) the RD in all grass species. However, there was a marginal decline in diameter on the fifth sampling date for all the grass species.

Overall, *D. macroblephara* had a significantly higher ($p<0.05$) RTD than the other two grass species, with *P. mezianum* having the lowest.

Differences in SRL were significant ($p<0.05$) among the grass species with *D. macroblephara* having the highest SRL and *P. mezianum* having the lowest on all the sampling dates. Generally, decreases in soil moisture content resulted in increase in SRL.

Soil moisture content variation had a significant ($p<0.05$) effect on the RDMC, with the lowest being observed on the first and third sampling dates when soil moisture was highest.

**Table 4. 1. Average root diameter (mm), root tissue density (g cm$^{-3}$), specific root length (m g$^{-1}$), and root dry matter content (%) of the three grass species across sampling dates.**

| **Sampling dates** | **1** | **2** | **3** | **4** | **5** |
|---|---|---|---|---|---|
| **Root diameter (mm)** | | | | | |
| *D. macroblephara* | $0.68^{cdef}\pm0.03$ | $0.58^{def}\pm0.03$ | $0.52^{f}\pm0.03$ | $0.55^{ef}\pm0.06$ | $0.51^{f}\pm0.03$ |
| *P. mezianum* | $1.33^{a}\pm0.14$ | $1.39^{a}\pm0.10$ | $1.24^{a}\pm0.06$ | $1.18^{a}\pm0.17$ | $1.15^{ab}\pm0.09$ |
| *T. triandra* | $0.63^{cdef}\pm0.05$ | $0.88^{bc}\pm0.08$ | $0.80^{cde}\pm0.10$ | $0.83^{cd}\pm0.14$ | $0.76^{cdef}\pm0.08$ |
| **Root tissue density (g cm$^{-3}$)** | | | | | |
| *D. macroblephara* | $0.4697^{ab}\pm0.061$ | $0.5604^{a}\pm0.0388$ | $0.4159^{ab}\pm0.1666$ | $0.4428^{ab}\pm0.1471$ | $0.5910^{a}\pm0.1356$ |
| *P. mezianum* | $0.0772^{c}\pm0.0364$ | $0.0562^{c}\pm0.0308$ | $0.2453^{bc}\pm0.0711$ | $0.2286^{bc}\pm0.0210$ | $0.2625^{bc}\pm0.0319$ |
| *T. triandra* | $0.6818^{a}\pm0.069$ | $0.0972^{c}\pm0.0830$ | $0.2236^{bc}\pm0.1259$ | $0.2807^{bc}\pm0.0489$ | $0.4667^{ab}\pm0.114$ |
| **Specific root length (m g$^{-1}$)** | | | | | |
| *D. macroblephara* | $347.89^{cde}\pm39.32$ | $422.61^{bc}\pm 14.66$ | $392.39^{cd}\pm39.48$ | $504.11^{ab}\pm3.12$ | $551.68^{a}\pm39.40$ |

| | | | | | |
|---|---|---|---|---|---|
| *P. mezianum* | 163.67$^{g}$±30.43 | 217.57$^{fg}$±12.92 | 168.28$^{g}$±10.06 | 197.07$^{g}$±46.02 | 209.29$^{fg}$±30.32 |
| *T. triandra* | 306.33$^{de}$±31.66 | 348.51$^{cde}$±42.77 | 324.32$^{de}$±11.80 | 287.92$^{ef}$±13.15 | 326.94$^{de}$±4.93 |
| **Root dry matter (%)** | | | | | |
| *D. macroblephara* | 20.27$^{d}$±1.57 | 38.61$^{c}$±3.41 | 25.19$^{d}$±3.21 | 52.04$^{b}$±5.52 | 69.50$^{a}$±4.52 |
| *P. mezianum* | 24.30$^{d}$±4.21 | 40.42$^{bc}$±2.07 | 23.99$^{d}$±4.27 | 44.38$^{bc}$±4.82 | 76.32$^{a}$±1.40 |
| *T. triandra* | 21.93$^{d}$±1.83 | 44.86$^{bc}$±7.73 | 19.95$^{d}$±1.46 | 50.89$^{b}$±5.43 | 70.92$^{a}$±1.97 |

*Means within the same row and column with different superscripts are significantly different at $p<0.05$, ±Standard Deviation*

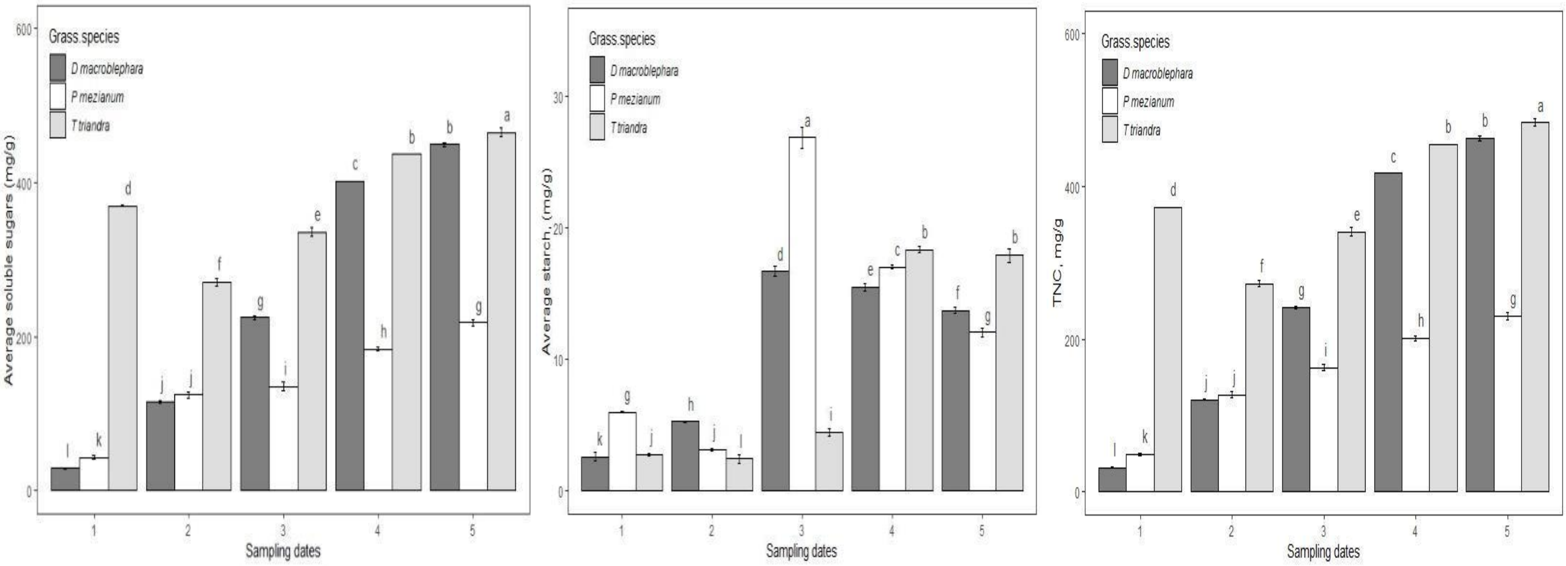
### 4.1.4 Effect of soil moisture variation on total soluble sugars, starch, and non-structural carbohydrate

Figure 4.3. represents the TSS, starch, and NSC contents across the three grass species at different soil moisture contents. The three parameters were significantly ($p<0.05$) affected by changes in soil moisture content in all the three grass species. Interactions between the grass species and soil moisture content were also significant ($p<0.05$).

Overall, *T. triandra* had the highest TSS content while *P. mezianum* had the lowest. However, TSS contents increased when soil moisture contents decreased across all the three grass species (Figure 4.3a). It was highest on the fifth sampling date in all the grass species (449, 218, and 465 mg g$^{-1}$ for *D. macroblephara, P. mezianum,* and *T. triandra*, respectively).

*P. mezianum*had the highest starch content (26.88 mg g$^{-1}$) on the third sampling date (Figure 4.3b), while *T. triandra* had the lowest content (2.46mg g$^{-1}$) on the second sampling date.

Generally, NSC increased with decrease in soil moisture content across all the grass species. *T. triandra* had the highest NSC content across all the sampling dates, with the highest NSC content (483.49 mg g$^{-1}$) being recorded on the fifth sampling date (Figure 4.3c). *D. macroblephara* had the lowest NSC content on the first and second sampling dates while *P. mezianum* had the lowest level on the third, fourth and fifth sampling dates.



a) b) c)

**Figure 4. 3. Average total soluble sugars (TSS) (a), starch (b), and NSC (c) across grass species and different soil moisture contents**
*Bars with different letters are significantly different at $p<0.05$.*

### 4.1.5 Pearson correlation coefficients for roots, bud, and carbohydrate parameters across the three grass species

There was a consistent negative correlation between the number of buds per tiller and bud sizes with tiller height (r= -0.52 and r=-0.68, respectively) and SRL (r=-0.58 and r=-0.63, respectively). Bud sizes were negatively correlated with NSC (r=-0.8), while NSC was positively correlated with tiller height and PRDM (r=0.73 and r=0.52, respectively). RTD and SRL were negatively correlated to RD (r=-0.81 and r=-0.88, respectively).

**Table 4. 2. Pearson correlation coefficients (r) or root morphological parameters, below-ground bud parameters, between root parameters and NSC, and between below-ground buds and NSC**

| | NSC | Tiller Height | Average Root Diameter | Buds/Tiller | Bud sizes | Root Tissue density | Specific Root length | PRDM |
|---|---|---|---|---|---|---|---|---|
| NSC | | 0.7333** | -0.4976 | -0.5861 | -0.8042*** | 0.3860 | 0.4863 | 0.5277* |
| Tiller Height | | | -0.2702 | -0.527* | -0.6873** | -0.0156 | 0.1984 | 0.4258 |
| Average Root Diameter | | | | 0.5752* | 0.7580** | -0.8139*** | -0.8860*** | -0.0577 |
| Buds/Tiller | | | | | 0.6269* | -0.3897 | -0.5836* | -0.2682 |
| Bud sizes | | | | | | -0.5798* | -0.6343* | -0.2811 |
| Root Tissue density | | | | | | | 0.6472* | 0.0971 |
| Specific Root length | | | | | | | | 0.2453 |
| PRDM | | | | | | | | |

Level of significance: ***= P <0.001, ** = P < 0.01, * = P < 0.05

## 4.2 Discussions

### 4.2.1 Effects of soil moisture variability on bud numbers and size

Significant differences in the number of buds among the three grass species was not a surprise since they are genetically different. For instance, *P. mezianum* is a rhizomatous grass with long rhizomes, and grasses with these growth characteristics have been shown to have relatively more below-ground buds (Zhang *et al.*, 2009; Ott and Hartnett, 2015) than those with different growth characteristics. The buds are the organs that give rise to new tillers in grasses which replace the ones that have died off due to old age or been grazed off. Therefore, buds impart persistence on perennial grasses (Hendrickson and Briske, 1997) and the capacity to withstand grazing. *D. macroblephara*, on the other hand, has horizontal extravaginal stolons of varying lengths, while *T. triandra* is a tufted perennial grass characterised by upright bud growth (intravaginal outgrowth), resulting in many new shoots next to the parent plant.

Studies on below-ground buds are few in SSA, where the three grasses studied here are predominant. The few notable studies include Hartentt *et al.* (2006) and Dalgleish *et al.* (2012) which focus on perennial grasses of the Kalahari sandveld region of Botswana. Among grasses of the same genus with similar growth characteristics, the number of buds per tiller lies within the range found in this study. Dalgleish *et al.* (2012) reported that *P macrourum* had a higher number of buds per tiller (3.0) than many other species (*Aristida species*, *E cylindriflora*, *P squarrosa*, and *P patens*). In the same study, *D eriantha* was found to have 2.5 buds per tiller, similar to the number of buds in *D. macroblephara*.

The high number of buds per tiller in *P. mezianum* suggests that the grass is more resilient to the vagaries of nature than most of its contemporaries. A large bud bank ensures a rapid increase in species population by producing a high number of new tillers when conditions are favourable as they capitalize on periods of high resource availability. In addition, large bud banks are natural adaptive mechanisms against environmental variability since, among other things, they enhance the compensatory growth of the grass following grazing (Hartnett *et al.*, 2006). Besides *P. mezianum* having a higher number of buds, they were vertically distributed around the tiller bases, reducing the chances of being damaged by fire, hoof action, or grazing. The findings of this study are at variance with those of Dalgleish *et al.* (2012), which concluded that drought-tolerant species have relatively small bud banks and that other factors such as bud longevity or seed banks play a bigger role. For species with relatively small belowground bud banks such as *D. macroblephara* and *T. triandra,* tiller recruitment is slow and limits their ability to respond to grazing and other activities (Russell *et al.*, 2015). For such grass species, the ability to recover from resource stresses imposed by abiotic factors like droughts, fires, pests, etc is limited. In this study, although *T. triandra* had the lowest number of buds, it had the highest percentage of flowering tillers. The combination of a high number of flowering tillers and fewer buds per tiller in *T. triandra* suggests a dual strategy of population resilience through both the seeds and buds, with a greater dependency on seed reproduction (Hartnett *et al*., 2006). High seed production and successful seedling establishment in *T. triandra* may give it higher resilience and persistence against frequent environmental disturbances. All the same, seed banks are crucial in genetic conservation as they increase the capacity of plants to adapt to environmental changes (Hartnett *et al.*, 2006). Similar bud anatomy and morphological patterns have been observed in *S uniplumis*, *E lehmanniana*, and *A stipitata* (Hartnett *et al.*, 2006).

The relationship between bud numbers per tiller and soil moisture content tended to be species-specific. Thus, within normal soil moisture regimes, species with low average number of buds per tiller will never exceed those with higher numbers on average. The maximum numbers are genetically fixed. For instance, *P. mezianum* had the lowest number of buds when soil moisture content was highest, while the opposite was the case in *T. triandra*. *P. mezianum* had more dormant buds activated to form new tillers when moisture content was high, with a greater proportion of buds transitioning to dormancy with significant drop in soil moisture content. Similar results were reported in *B gracilis* (Russell *et al*., 2017)and *A gerardii* (Ott and Hartnett, 2012), where more buds transitioned to dormancy with increase in soil moisture deficit. The maintenance of a large number of buds in the dormant state protects local grass species from impacts of unfavourable conditions such as droughts (Dalgleish *et al*., 2012). For *T. triandra,* the buds rarely go dormant because they transition to new tillers as soon as they are formed. This is the same in *D oligosanthes,* which maintains a smaller proportion of dormant buds throughout the season (Ott and Hartnett, 2012). This means that the highest number of buds per tiller will most likely be observed when the bud formation process is at its peak, which coincides with the highest soil moisture content. *D. macroblephara* exhibited a steady number of buds per tiller even under severe soil moisture deficit, an observation which agreed with the findings of VanderWeide and Hartnett. (2015) while working with grasses and forbs of tallgrass prairie during a two-year drought period in the tallgrass prairie of northeast Kansas, and Busso *et al.* (2011) under moderate to heavy defoliation of *Poa ligularis* grass species.

Large bud sizes, as demonstrated by *P. mezianum,* have been associated with a well-developed and active vascular connectivity with the polar auxin transport system (PATS), which increases auxin export and nutrient import into the bud (Waldie *et al.,* 2010). This suggests that more resources are stored in these buds, ensuring a higher survival rate and competitiveness during the early phase of ontogenesis (Wu *et al*., 2021). Grass species with larger buds could also have longer bud longevity, leading to a large bud bank comprising multiple-year cohorts. This is important since tillers produced in any year will be influenced by the size and number of buds produced in the previous years under prevailing disturbances and/or resource variations. Accumulation of buds over several years buffers a grass stand from fluctuations across years. *T. triandra* and *D. macroblephara* had smaller bud sizes that possibly lived for only one year, with tiller recruitment coming from the current year's buds. These grass species are more adept to environmental changes as they can closely track inter-annual environmental changes (Ott *et al*., 2019). The decrease in bud size with increase in water deficit can be attributed to reduction in water supply to buds resulting in decrease in turgor pressure. Moisture deficit also slows down photosynthesis, growth and development of all plants parts. For example, when resources are unlimited, the plant distributes resources to all organs optimally. However, when there is a constraint in resources, the plant prioritizes the most delicate organs and reduces supply to other organs. Our results are in agreement with those of Pembleton *et al*. (2010), which showed that species that experienced moisture deficit had smaller buds.

### 4.2.2 Effects of soil moisture variability on tiller height

Differences in tiller heights among the grass species were also not surprising since again the three grass species are genetically and morphologically different. For instance, *P. mezianum* is a stout rhizomatous grass that is slow-growing, while *D. macroblephara* is a stoloniferous bunchgrass that forms open tufts from a knotty rootstock and is characterised by a creeping growth characteristic. *T. triandra,* on the other hand, has an erect tufted culm and grows relatively faster than most of its contemporaries. Fast-growing species with erect culms are usually taller than the slow-growing species with semi-erect culms. They have been shown to have a competitive advantage over others, as they use resources more efficiently (Mganga, 2009). However, *T. triandra,* with its vertical growth characteristic, is more likely to be depleted first when there is overgrazing since it is more accessible than *D. macroblephara*. Nevertheless, *T. triandra's* rapid growth rate enables it to out-compete other species for water, light, and nutrients (Dunning *et al*., 2017).

The progressive increase in tiller height with grass maturity was expected since it is a function of growth and development of all living organisms. Similar results were reported by Machogu (2013), Koech *et al*. (2016), and Kamau (2020). The negative relationship between tiller height, number of buds per tiller, and bud sizes suggest that when plants invest a larger proportion of their resources in increasing bud numbers and sizes, less resources are available for rapid growth and plant biomass. This was confirmed by the negative relationship between NSC in roots and bud sizes in our study. Bud banks are highly resource-dependent, and the reserves stored in the buds are used for resprouting and supporting the parent plant (Bell and

Ojeda, 1999). Also, a large bud size will likely lead to stout tillers, which take longer to establish.

### 4.2.3 Effects of soil moisture variability on root diameter, root tissue density, specific root length, and root dry matter content

Differences in RD among the three grasses were expected due to their distinct genetic differences. However, grass species with a large RD have a higher resource storage capacity, transport more water, and have stronger soil-penetrating ability to access deeper layers in drying soil conditions (Davies and Bacon, 2003). In addition, thicker roots generally have a lower turnover rate, longer lifespan, and larger cross-sectional areas, making them more resistant to external stress factors (Gu *et al.*, 2011). On the other hand, species with a large RD have been shown to have a low moisture uptake (Roumet *et al.*, 2011). However, they can maintain high water uptake over a longer time and, hence, survive with less water during dry seasons (Ji *et al.*, 2020). *D. macroblephara* and *T. triandra* with smaller RD were observed to be laterally oriented, meaning that they were best adapted to utilize soil moisture content in the upper soil profile. Grasses with small RD tend to acquire resources faster which is advantageous under soil moisture deficit conditions (Fort *et al.*, 2013). These grasses also have a high nutrient uptake, rendering them more adaptable to rapid growth and establishment at the onset of the rains. Similar to this study, several previous studies have reported a marginal decrease in RD with increased soil moisture deficit; this is attributed to improved nutrient and water acquisition (Fuentealba *et al.*, 2015; Ma *et al.*, 2018).

RTD is a fundamental trait in comparative root ecology, being increasingly used as an indicator of plant species resource use strategy. Low RTD has been associated with fast-growing species in nutrient-rich habitats (Wahl and Ryser, 2000). Contrary to our expectation, *P. mezianum* had the lowest RTD among the three grass species. This was attributed to several characteristics of its roots. First, *P. mezianum* roots were found to have a relatively thick outside coat which increased their volume. Second, the low RTD could be accounted for by the relatively high water content in its roots. For *T. triandra* and *D. macroblephara,* the slight increase in RTD with increase in moisture deficit meant that more resources were being directed towards root development than above-ground growth. This also meant that when there is sufficient moisture, these grasses develop low-density roots, which are formed relatively faster and result in rapid above-ground biomass development. However, as soil moisture deficit increases, more focus is given to more dense roots with longer lifespans.

SRL is the ratio between root length and root mass and reflects the root's efficiency in exploring the soil in search of nutrients and water (Hernández *et al*., 2010). In this study, *T. triandra* and *D. macroblephara* had the highest SRL. In contrast, *P. mezianum* had the least SRL, suggesting that *T. triandra* and *D. macroblephara* has a more efficient water acquisition strategy. A high SRL (thinner roots) facilitates better exploration of the soil profile for water, leading to increased overall root hydraulic conductance (Hernández *et al*., 2010). This was further supported by the negative relationship between RD and SRL in this study. SRL has also been associated with higher nitrogen uptake rates (Reich *et al*., 1998), root respiration (Liu *et al*., 2020), and shorter root lifespan (Ryser, 2006). High SRL is generally recorded in fast-growing plant species, which is closely associated with a high root turnover, root elongation rate, and high nutrient uptake, which is a function of the root surface area (Leuschner *et al*., 2013; Freschet *et al*., 2015). Similar results were reported by Fort *et al.* (2013) in their study of root and leaf functional traits of eleven perennial temperate grasses. The less drought-tolerant species were found to have a high SRL and high N uptake, while the more drought-tolerant species had a low SRL. *P. mezianum* with a lower SRL meant that the root turnover was low, and a higher investment of resources per unit length was needed to ensure longevity of the current season’s roots (Eissenstat *et al*., 2000). In other words, the root growth strategy of *P. mezianum* was more resource-conservative due to thicker roots, which enhanced soil penetration as the profile dried up (Davies and Bacon, 2003). Low SRL, however, meant that less soil volume was explored for water and nutrient acquisition.

In *D. macroblephara,* SRL increased with increase in soil moisture deficit, while *T. triandra* and *P. mezianum* maintained a constant SRL with increase in soil moisture deficit. Kadam *et al*. (2015) reported conflicting findings from their study on rice and wheat tolerance to water deficit. In rice, the SRL increased with increase in water deficit, but in wheat, the opposite was true. Significant decrease in SRL in wheat cultivars was attributed to increase in average root thickness and total root weight density. Similarly, de Vries *et al.* (2016) in their study on grassland species under controlled conditions, reported a decrease in SRL with increase in moisture deficit in *A adorotum* and *L hispidus*, while it increased in *R acetosa* and remained constant in *D glomerata*. Contrary results were reported by Ji *et al*. (2020), who in their study on synergistic fluctuations in root traits and NSC concentrations of temperate tree species under diverse environmental conditions, reported that SRL increased with increase in drought intensity in *J mandshurica, F mandshurica,* and *P amurense.*

As expected, PRDM increased with an increase in soil moisture deficit. Being a ratio of dry weight: fresh weight, it is expected that the moisture content in plants will decrease as it decreases in the soil. Liu *et al*. (2020) reported an increase in root carbon allocation with increase in moisture deficit, which contributes to an increase in PRDM. In addition, increase in PRDM was attributed to an increase in NSC, which increased as moisture deficit increased. This was confirmed by the positive relationship between NSC and PRDM in our study.High PRDM has been linked to high inorganic N, which would cause high N availability in the soil due to decreased uptake from the soil (de Vries *et al.*, 2016). Pérez-Ramos *et al*. (2012) reported a positive correlation between PRDM, leaf thickness, and leaf dry matter content. They linked the high PRDM to water use efficiency and low SRL.

### 4.2.3 Effect of soil moisture variability on TSS, starch, and NSC

It is common knowledge that soluble sugars are the main solutes that provide structural materials and energy required to respond to disturbances in an ecosystem (Morkunas and Ratajczak, 2014). High soluble sugars ensure grasses grow rapidly at the onset of the rainy season and that they are well adapted to the erratic rainfall patterns common in many rangelands (Priyadarshini *et al.*, 2016). For *P. mezianum*, the low soluble sugar content can explain its slow growth rate.The increase in soluble sugars with the increase in soil moisture deficit was expected as the plant prioritizes storing more sugars in the roots for the next growing season. This was attributed to the fact that roots are the primary nutrient acquiring and storing organs, and as such, the reserved carbohydrates will increase as soil moisture content decreases (Snyman, 2009). The stored sugars ensure the emergence of new tillers at the onset of rains (Guo *et al*., 2020). This might explain why grasses grow rapidly at the onset of rains, even when there was limited soil moisture a few days before. Increase in soluble sugars has been interpreted as a way of increasing osmotic potential under moisture deficit conditions (Hasibeder*et al*., 2015). Our results are in agreement with those of Priyadarshini *et al*. (2016), who looked at the interactions between trees and perennial grasses on root characteristics of range grasses in the ASALs of South Africa. Similar results were reported by Guo *et al*. (2020) who in their study on perennial ryegrass seedlings reported increased sugar levels in roots under moisture deficit conditions.

Starch is the major reserve carbohydrate for tillering and regrowth of grasses and also acts as a buffer for drought-instigated disparities that occur during resource acquisition by photosynthesis and carbon-sink activities (Muller *et al*., 2011). Starch levels were quite low in our study and formed a small fraction of the NSC. Similar results were reported by Priyadarshini *et al*. (2016) in their work on C4 grass species. They reported low starch contents in the NSC in three study sites in South Africa. Guo *et al*. (2020) reported that starch content did not change significantly in roots but significantly decreased in shoots under drought conditions, possibly because the grasses allocated more carbon for storage in roots in addition to the amount required for growth. Despite the low starch content in NSC, it is crucial for long-term storage. Its importance comes into play when there is an extended period of moisture deficit (Busso *et al.*, 1990).

NSC plays an important role in regulating key physiological activities of plants, including buffering the plants from adverse environmental conditions (Ji *et al.*, 2020). Physiological activities include nutrient absorption, respiration, organic secretion, and plant growth. In addition, NSC plays an important role in plant defense, metabolism, delaying or preventing plant death, and drought resistance (Ji *et al.*, 2020). Our study shows that *T. triandra* had the highest NSC content, which might partially explain its relatively fast growth rate. Ji *et al.* (2020) observed that plants with thinner root diameter had higher soluble sugars than roots with a thicker diameter, as in the case of *T. triandra* in our study. NSC increased gradually in all three grass species with increase in moisture deficit. Under moisture deficit, NSC in roots has been shown to increase at the expense of the amount in shoots, which is thought to facilitate the emergence of new tillers at the onset of rains (Guo *et al.*, 2020). It has also been reported in instances where C uptake is severely limited, with priority being given to belowground carbon storage over above-ground storage (Bahn *et al.*, 2013). This paradigmatic shift is necessitated by the preparation for the next season's growth, which will require high energy resources to enable growth. This energy is used to activate buds to enable new tiller growth to the point where new leaves are formed to produce their own food. Oosthuizen and Snyman. (2003) reported high amounts of NSC in *T. triandra* and an increase of up to 25% of it under moisture deficit. Busso et al. (1990), in their study with some North American grass species, reported an increase of up to 7 times in below-ground NSC in both clipped and unclipped plants under severe moisture deficit. It was theorized that the surge in

NSC was in preparation for the rapid initial regrowth once favorable soil moisture conditions resumed (Hasibeder *et al*., 2015). NSC has been shown to remain relatively high in the early days after cessation of drought, thus ensuring the successful formation of new tillers (Guo *et al*., 2020). Contrary to our study, (Ji *et al.*, 2020) reported root tip soluble sugars, starch, and starch to decrease with increased moisture deficit in their study on the roots of temperate trees.

# CHAPTER FIVE

# CONCLUSIONS AND RECOMMENDATIONS

## Conclusion

Water is an indispensable element for animal and plant life as it is part of their tissues with some of them being more than 90% water. Water is a critical ingredient in photosynthesis since it is required for translocation of nutrients and dissipation of heat. Therefore, change in its content in a plant’s environment is transmitted to all other parts of the plant. The results of this study confirmed that soil moisture variation affects all the parts of a plant. Too little moisture content in the soil and hence in the plant results in damaged cells, tissues and organs, and in extreme cases, even death of the plant. On the other hand, too much moisture causes the accumulation of toxic compounds and diseases such as root and crown rot.

This study demonstrates that below-ground buds and roots play an important role in above-ground vegetation dynamics, with patterns of variability in these parts being associated with changes in soil moisture content. The ASALs are characterized by erratic rainfall and the variation in soil moisture content in this study did not come as a surprise. The number of buds in *P. mezianum* increased as soil moisture content decreased, while it decreased in *T. triandra* and remained constant in *D. macroblephara.* The maintenance of a large number of buds buffers *P. mezianum* from impacts of unfavourable conditions such as drought.

This study also showed that grasses will respond to moisture deficit by having thicker roots with longer lifespans and more penetrating power. *P. mezianum* had the largest roots enabling it to go to deeper soil profile to facilitate water and nutrient uptake. Furthermore, the fast-growing species, *T. triandra* and *D. macroblephara* had a high specific root length and narrow root diameter which enables them to absorb water and nutrients relatively fast and from small pockets of soil. Further, NSC will increase when there is some form of moisture deficit in grasses in preparation for the next season's growth. The high NSC in *T. triandra* and *D. macroblephara* contributed to the emergence of new tillers and their fast growth.

In summary, this study provides a good insight into how range grasses are adapted to and respond to moisture variation. It is the most important factor in the growth of all living organisms, and it is found in every cell. Therefore, different patterns of below-ground buds and root functional traits among grasses may help explain changes in grass species composition and community structure in response to moisture variability.

**Recommendations**

Based on the findings of this study, the following recommendations can be made:

1. The management of rangelands should allow a period of undisturbed growth for carbohydrate reserves replenishment and restoration from below-ground buds after a period of disturbance in order to obtain sustainable production. In case of a severe degradation where buds and crown reserves have been depleted, reseeding should be done.
2. Grass species that have a high number of buds, high root reserves, and are highly palatable should be given preference when replanting as they offer a greater chance of recovery after disturbance.
3. To improve understanding of how below-ground plant organs influence the rangeland ecosystem:
   a. Studies should be conducted with more species from different geographical areas.
   b. Studies should also be carried out across several seasons to give a better picture of how soil moisture variation and/or climate change affect these

below-ground parts.

c. More detailed quantification of bud and seed demography should be investigated to assess the relative importance and roles of seed and vegetative reproduction.
d. The combined effect of soil moisture variation and defoliation on below-ground parts should be investigated.

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