

ASSESSING THE QUALITY OF FORAGE FOR LIVESTOCK IN A SEMI-ARID PASTORAL SYSTEM IN SOUTH AFRICA

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The degree of Master of Science

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DECLARATION

I declare that "Assessing the Quality of Forage for Livestock in a Semi-Arid Pastoral System in South Africa" is my own work. It is submitted in partial fulfilment of the requirements for the degree of Masters in Science at the Science Faculty, University of the Western Cape. It has not been submitted for any degree or examination at any other university. All references and sources of information to my knowledge are accurately reported.

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DEDICATION

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ABSTRACT

This study evaluated the nutritional quality of the forage plants in Namaqualand Granite Renosterveld vegetation in the Kamiesberg uplands of the Leliefontein communal area, South Africa. Determining the quality of forages is one of the most important factors necessary for the effective management of rangelands as it impacts on the nutrient needs of animals and consequently, the grazing capacity in rangelands. The edible portions of various forage plants were collected in the wet and dry seasons in 2012 and 2013 after which the nutritional quality (mineral nutrient content; crude protein (CP); fibre, neutral detergent fibre (NDF) and acid detergent fibre (ADF); dry matter digestibility (DMD); dry matter intake (DMI); metabolizeable energy (ME); and relative forage value (RFV)) as well as the anti-nutritional quality (total phenolics (TP); condensed tannins (CT); and silicon (Si) concentrations) of the plants were determined. Plants were thereafter grouped into their respective growth forms: grasses (15 species), herbs (15 species), leaf succulents (17 species), non-succulents (134 species), reeds (7 species), trees (8 species) and stem succulents (2 species) for statistical analyses.

There were generally only a few significant differences for each forage growth form, when comparing the nutritional and anti-nutritional qualities between the two seasons. Certain forage types such as leaf succulents were found to have a high nutritional value in terms of their mineral nutrient content, CP, DMD and ME, but were also found to contain high concentrations of one or more anti-nutritional factors. However, within each season, results showed that for both the nutritional quality and anti-nutritional quality, there was a significant difference between the different growth forms within each season. This suggests that both of these quality parameters are essential in order to draw meaningful conclusions regarding forage quality of these semi-arid rangeland plants. Further research is needed at the species level to determine what plant species are the most nutritious in terms of both nutritional and anti-nutritional quality in order to inform the potential production of these species on a commercial scale.

KEYWORDS

Forage quality, Mineral nutrients, Crude protein, Dry matter digestibility, Metabolizeable energy, Total phenolics, Condensed tannins



CHAPTER ONE

INTRODUCTION AND LITERATURE REVIEW

1.1 Arid and semi-arid environments

Arid and semi-arid regions of the world cover more than 30% of Earth's land surface. Arid and semi-arid ecosystems are distinguished by irregularity in rainfall (Samuels, 2013) and temperature extremes between maximum and minimum temperatures. The United Nations has defined semi-arid regions in climatic terms as those areas where the ratio between precipitation and potential evapotranspiration is between 0.21 and 0.50 (Ribot et al., 1996). In general, rainfall in semi-arid areas is between 200 and 500 mm per year, and the year to year variability is comparatively large at \pm 20-30% of the annual mean (Ribot et al., 1996). South Africa is generally regarded as semi-arid with a mean annual rainfall of roughly 450 mm. However, the country has a wide variation in annual rainfall from less than 50 mm to more than 3 000 mm in different regions (Palmer and Ainslie, 2006).

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Rainfall variability can exert a strong effect on rangeland production and species composition (Fynn and Connor, 2000). Plant and animal diversity is connected spatially and temporally in various arid environments (Milton and Dean, 2010), and productivity generally increases linearly with precipitation (Sullivan and Rohde, 2002). Irregular rainfall distribution also leads to fluctuations in the quantity and quality of available forage for herbivores (Abusuwar and Ahmed, 2010). The nutritional quality of forage plants changes with season (Marshal et al., 2005). Rainfall also affects the mineral composition of forage plants in rangelands. For example, calcium tends to accumulate in plants during periods of drought, but when the soil moisture is high it is presented in smaller concentrations as result of decreased water content. In contrast, phosphorus is present in higher concentrations when the rainfall is high (McDonald et al. 2010).

1.2 Grazing of rangelands

Due to the variability of rangeland resources in semi-arid areas, livestock farming is regarded as the best land to make optimal use of the heterogeneity in resources (Samuels, 2013). Pastoralism is an adaptation to resource heterogeneity in semi-arid areas as herds are moved between grazing areas in search of better quality forage (Samuels, 2013). Livestock is thus an essential component of the ecology in semi-arid rangelands in Africa (Turner and Hiernaux, 2002; Strauch et al., 2009). Economically, livestock is also estimated to contribute to the livelihood of at least 70% of the world's poor population including those in semi-arid regions (Ngqangweni and Delgado, 2003).

In developing countries, the livestock industry has become one of the main focus areas for the development of its economies (Upton, 2004). Livestock in developing countries is one of the fastest growing agricultural subsectors; it forms 33% of the agricultural gross domestic product (GDP) in the developing countries in general and is rapidly increasing demand for livestock products (Swanepoel, 2010; Thornton, 2010). In South Africa, for instance, more than 80% of the natural vegetation is under management for livestock production (Du Toit et al., 1991) and approximately 70% is suitable for extensive livestock farming (Scholtz et al., 2013) including the communal areas which occupy 17% of the total farming areas in the country (Palmer and Ainslie, 2006). The implementation of the South African Land Redistribution and Agricultural Development (LRAD) policy has made sufficient progress so as to give pastoralists access to additional land to reduce poverty, promote economic improvement and provide pastoralists with the opportunity to increase their livestock numbers (Rohde et al., 2006).

1.3 Pastoralism- an adaptation to resource variability

While some of the general goals of pastoral systems are to raise livestock, and maintain their overall good quality for reproduction and marketing purposes, pastoralists also seek to maintain or even increase the available above-ground forage to reduce soil erosion (Archer, 2004). Pastoral strategies reduce the impacts of adverse climatic conditions on the pastoralists and their livestock through adaptive management (Speranza, 2010; Samuels, 2013). Pastoralism permits

people in arid and semi-arid areas to cope with the high climatic variability and to respond effectively to socio-political and economic pressures (Hesse and Cotula, 2006; Samuels, 2013).

Pastoralists typically select rangelands which have suitable rangeland quality for the livestock in order to increase productivity. However, in rangelands with unfavourable plants species, livestock overgraze the desirable plants causing rangeland degradation (Dabasso et al., 2012). Heavy grazing due to high stocking rates in the communal areas has also resulted in significant changes in the vegetation in Namaqualand, from a perennial to annual dominated rangeland (Todd and Hoffman, 2009). Changes in vegetation diversity have attracted many researchers to address the relationship between intensive livestock grazing and changes in the quality of vegetation in communal pastures in Africa (Dabasso et al., 2012).

In arid environments, inappropriate management techniques to livestock grazing lead to a reduction in natural resources such as forage diversity (Strauch et al., 2009). There is an interaction between grazing animals and landscape dynamics: therefore, proper management of pastoral systems is required to make appropriate decisions for the sustainable use of arid rangelands (Ruiz-Fernández et al., 2007).

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1.4 Forage quality

1.4.1 Importance of forage quality for pastoral livestock

Forage quality is defined as the capacity of forage to provide the required nutrients to livestock (Muir et al., 2007; Newman et al., 2009; Adesogan et al., 2011). Forage quality is a direct reflection of essential nutrient content and availability to the consuming animal (Ortmann et al., 2006; Minson, 2012). Forage quality includes the nutritive value and forage intake (Newman et al., 2009). Knowledge about the quality of forage in rangelands is important to determine the grazing capacity in the rangeland (Godari et al., 2013). Forage quality is also significant because it is linked to animal performance (Pinkerton and Cross, 1991). Reaching high levels of animal performance and health are dependent on high quality nutrition (Corson et al., 1999) and the failure to meet minimum nutritional requirements of the animals leads to a decrease in animal production such as milk, weight and reproductive rates, and to susceptibility to diseases (Olson et

al., 2010). Furthermore, the quality of forage changes at local scales between different soil types, at larger scales from one region to another and at temporal scales from season to season based on the type of vegetation cover (Godari et al., 2013). Thus, understanding the spatial and temporal changes in forage quality in the rangeland is essential for livestock farmers.

The concept of forage quality stems from the interaction between the physicochemical properties of plants and the animals' physiological ability for ingestion, digestion, nutrient absorption and utilisation (Illius and Allen, 1994). Analysis of forage quality is important because forage quality is affected by several factors such as forage genotype, plant maturity, season, anti-nutritional quality factors and management (Adesogan et al., 2011). For example, legumes are higher in protein and calcium compared to grass forages of the same maturity (Gomez, 2011; Njidda et al., 2012).

In order to maximise diet quality, animals need to feed on plants to gain nutrients and energy for maintenance, growth and reproduction requirements when foraging (Doucet and Fryxell, 1993; Iason and Villalba, 2006). According to Provenza and Launchbaugh (1999), herbivores learn food selection behaviours and their choices are influenced by both toxins and nutrients in foods. Animals generally consume forage that is higher in nutrients and lower in toxins, and also tend to feed selectively among plant species, plant parts and foraging locations (Provenza and Launchbaugh, 1999). Therefore, variation in feed quality and quantity in rangelands lead to variation in livestock performance; furthermore, livestock farmers are aware of its significance (Corson et al., 1999; Amiri and Mohamed Shariff, 2012).

The selection of forages by the animals is based on the plants' palatability. Palatability can be explained as the hedonic response of an animal to its food in terms of flavour, texture and tasting (Provenza and Launchbaugh, 1999). Plant palatability can also be described as plants' attributes that change acceptability to animals, including chemical composition, growth stage and associated plants (Provenza and Launchbaugh, 1999). Thus, palatability is much more than a matter of taste; it is the interrelationship between a flavour of forage (smell, taste and texture), and its nutrient and toxin content (Burritt and Provenza, 2011).

Most research on forage plants has found that animals tend to select a mixed diet of forage plants (O'Reagain and Schwartz, 1995; Hendricks et al., 2002; Alonso et al., 2008; Estell et al., 2014).

However, according to Samuels et al. (2007), the availability of the amount of palatable plant species in a grazing area does not indicate that this area is rich in forage quality for livestock to graze as a high number of toxic plants are also available at the same time in the same area. Nevertheless, due to all rangeland plants containing some levels of secondary metabolites, it is not possible for livestock to avoid consuming toxic plants which include secondary compounds (Reed, 1998; Papachristou et al. (2005).

1.5 Nutritive value of forage

Forage nutritive value refers to inherent characteristics of consumed forage which determine its energy content (Newman et al., 2009). The forage nutritive value can be determined by the nutrient concentration, and nutrient and forage digestibility (Vendramini, 2010). There are many factors influencing the plants nutritive composition and thus, the nutritive value of the forages. These factors include the types of soil, water availability and climate variation (Andueza et al., 2010). Assessing the forage quality of rangelands can provide us with the knowledge of the forage nutritive value and livestock grazing capacity of the rangeland (Amiri and Mohamed Shariff, 2012). Proteins, fibre, and mineral elements such as phosphorous, potassium and calcium are all nutritional requirements for the well-being of the livestock (Brisibe et al., 2009; McDonald et al., 2010). Therefore, key aspects to consider when evaluating forages include the protein, fibre and mineral nutrient concentrations (Juárez et al., 2013).

1.5.1 Proteins

Proteins are complex organic compounds of high molecular weight and are found in all living cells (McDonald et al., 2010). Nitrogen is the main component of protein (Dasci et al., 2010) and accordingly, it makes up 60-80% of the gross nitrogen (N) of plants (Muir et al., 2007). The critical crude protein concentration for ruminants is roughly 7% (Dasci et al., 2010). Low protein concentrations in forage lead to protein deficiency, which is the most common deficiency in grazing livestock (Minson, 2012). Animals need a certain amount of proteins for growing new tissues (Miller, 2004), as well as for weight gain, growth and gestation (Muir et al., 2007).

Hence, inadequate protein in diet may cause anorexia, slow growth rate, decreased feed efficiency, decreased conception rate, low birth weight and lowered milk production (Minson, 2012). However, these deficiencies can be mitigated by feeding additional protein, non-protein nitrogen or a combination of both forms of supplements (Minson, 2012).

1.5.2 Fibre

The digestibility of forages is influenced by the fibre fraction of forages (McDonald et al., 2010). Forages vary extensively in fibre content, which is the best estimate of digestibility (Miller, 2004). Two types of fibre are commonly measured in forages, namely, neutral detergent fibre (NDF) and acid detergent fibre (ADF) (Miller 2004). The values of NDF represent the total fibre fraction (cellulose, hemicellulose and lignin) that form cell walls (structural carbohydrates or sugars) within the forage tissue (Ferreira and Mertens, 2007). Acid detergent fibre indicates the indigestible part of the fibre in the forage (Dasci et al., 2010) and is the best indicator of digestibility because it contains cellulose and lignin (Van Soest et al., 1991; 1994).

Generally, values of NDF differ amongst various forage plants. A higher NDF content is indicative of high total fibre in forages. Therefore, the lower the NDF value, the better for grazing animals. In addition, NDF content is also used to evaluate intake (the volume of the forage that the livestock will be able to consume) (Decruyenaere et al., 2009). A high content of hemicellulose is considered to provide a good source of energy to the animal (Arevalo et al., 2012). Various other forage quality indices can also be determined from the fibre contents, which includes dry matter digestibility (DMD). Dry matter digestibility is defined as the portion of the dry matter in a feed that is digested by animals at a specified level of feed intake (Collins et al., 2001). Furthermore, DMD measures the amount of energy that is available for the animals in the plant contents and is considered an important element of pasture nutritive value (Collins et al., 2001).

1.5.3 Mineral elements

Minerals are inorganic nutrients that are important in animal feeds because they play a vital role in the health and disease states of animals, but they do not provide any energy (Gonul et al., 2009; Lengarite et al., 2012) Minerals are classified as macro and micro (trace) elements. The requirements of macro-minerals which include calcium (Ca), phosphorus (P), sodium (Na), potassium (K), magnesium (Mg) and sulphur (S), and are required in amounts greater than 100mg/day. The amount required in micro-minerals which include iron (Fe), copper (Cu), cobalt (Co), , iodine (I), zinc (Zn), manganese (Mn), molybdenum (Mo), fluorine (F), chromium (Cr), selenium (Se) and chlorine (Cl) is less than 100mg/day (Soetan et al., 2010). Hence, the ingestion of sufficient amounts of forages by grazing animals is essential to meet their mineral requirements (Mirzaei, 2012).

Minerals such as Ca, P and Mg play a fundamental role in forming the structural components of the animals' organs and tissues (Suttle, 2010). Although minerals play an integral role in animal nutrition, it is important to note that some of them can be toxic, causing severe illness or death if given to the animal in excessive quantities (McDonald et al., 2010). This is particularly the case with micro-minerals such as Cu, Se, Mo and F. However, this study focused specifically on the quantities of macro-minerals in forage in semi-arid areas.

1.5.3.1 Sodium (Na) and Potassium (K)

Sodium (Na) and Potassium (K) perform mainly physiological functions that are concerned with the maintenance of an acid-base balance, membrane permeability and the osmotic control of water distribution in the animal's body. In addition, Na and K also assist with the function of the transmission of nerve impulses within the animal's body (McDonald et al., 2010), and play an important part in nerve and muscle excitability. Potassium, in particular, has been found to be engaged in carbohydrate metabolism and thus, the foliar content of K is generally very high (McDonald et al., 2010). Hence, K deficiency is rare in animals because they usually ingest large amounts thereof.

1.5.3.2 Calcium (Ca) and Phosphorus (P)

Calcium (Ca) is an important macro molecule found in the animals' body and is essential for the formation of the skeleton and teeth (McDonald et al., 2010). Calcium is essential for enzyme activity, especially for the transmission of nerve impulses and the contractile properties of muscle. Calcium deficiencies in adult animals cause osteomalacia, a deficiency where bones become weak and withdrawn (McDonald et al., 2010). Similarly, the physiological role of phosphorus (P) is essential in bone and teeth formation of animals, and about 80% of P is presented in bones and teeth (Suttle, 2010). Furthermore, P is important for glucose and glycerol absorption, formation of urine, metabolism of carbohydrates and protein (El Hag et al., 2015) and a deficiency thereof can also cause rickets and osteomalacia (Soetan et al., 2010). Phosporous is the most limiting mineral to animal productivity in many parts of the world (El Hag et al.et al., 2015).

1.6 Plant defences against herbivory

Plants respond to herbivore attacks through an intricate and variable system of defence (Coley et al., 2006; Rasmann and Agrawal, 2009). The evolution of chemical and mechanical defences in plants is due to herbivore pressure (Coley and Barone, 1996; Nepomuceno et al., 2013). Plants have developed a wide range of defence strategies to protect themselves against herbivores (Frost et al., 2008; Sebata and Ndlovu, 2012). These defence strategies are classified as physical defences and chemical defences (Frost et al., 2008). Physical defences are direct defences which exert a negative impact on herbivores' feeding and provide mechanical protection through spines, thorns, trichomes (leaf hairs), thicker leaves and cell wall thickness (War et al., 2012). Direct defences make it hard for livestock to access or consume forage plants (Moles et al., 2013).

Physical defences such as thorns and spines limit the amount of feeding by causing physical damage to the animal or by inducing allergic reactions (Hanley et al., 2007). In addition, physical defences reduce the forage intake that herbivores can consume per unit of time, thus, decreasing the palatability of forages (Papachristou et al., 2003). However, livestock such as goats are able to use their mobile upper lips to crop shoots and leaves protected by thorns and spines (Sebata

and Ndlovu, 2012). Trichomes (hair-like appendages) production protects the plant against damage from herbivorous insects (Dalin et al., 2008; Siahpoosh et al., 2015) by directly deterring the herbivores from feeding which conflicts the movement of insects on the plant surface (War et al., 2012).

Chemical defences are compounds stored in plants tissues that have effects either on digestion of plant biomass or have toxic effects on livestock after being absorbed after ingestion (Craine et al., 2003). Secondary compounds are the most widespread defences against different types of herbivores (Bergvall and Leimar, 2005). In forage plants there are various compounds such as tannins, nitrates, alkaloids and mycotoxins in many forages that can minimise animal performance, lead to sickness or even result in death (Tadele, 2015). The production of these components depends on the type of plant species. The concentrations of secondary compounds also vary by genotype, phenology (e.g. green versus senescent leaves) and season (Collins et al., 2001; Kraus et al., 2003).

1.6.1 Secondary compounds affecting forage quality of the

Secondary metabolites are classified into toxic and non-toxic compounds (Nepomuceno et al., 2013). Toxic compounds such as alkaloids and toxic amino acids have negative physiological effects such as reducing the nutrient utilisation and/or feed intake of plants when absorbed by animals (Barroso et al., 2001). Non-toxic compounds such as tannin cause decreased digestibility, palatability and animal selection (Schardl 2001; Bezemer and van Dam, 2005; Hattas et al., 2011; Mkhize et al., 2014).

1.6.2 Plant Phenolics

Phenolics are compounds distributed in the plant kingdom and are the most abundant secondary metabolites of plants. Plant phenolic compounds such as tannins influence ruminant health, nutrition, performance and environmental sustainability (Waghorn and McNabb, 2003). Tannins act within the animal's digestive tract by binding to the substrate to be digested, usually proteins;

thus, making them unavailable to ruminal microorganisms and impeding digestive enzymes (Dearing et al., 2005; Salem et al., 2006). Damage to the intestinal wall has been shown in small mammals following ingestion of tannic acid (Iason, 2005). Tannin's anti-nutritive effects are thus due to their ability to combine with dietary proteins (Salem et al., 2006), polymers such as cellulose, hemicellulose, pectin and minerals, and consequently, retarding digestion (Mcsweeney et al., 2001).

Tannins have both adverse and beneficial influences, depending on the tannin concentration and structure in plant species (Puchala et al., 2005). There are two types of tannins: hydrolysable and condensed tannins (CT) (Schofield et al., 2001; Njidda and Nasiru, 2010). The present study focused on CTs which are the most common type of tannin found in many types of forage plants (Min and Hart, 2003; Burritt and Provenza, 2011). Thus, determining total phenolics and CT provide more information of forage quality (Waghorn, 2008).

1.7 Location of the study

The focus of this study was the assessment of the quality of forage for livestock in the Leliefontein communal area, in a semi-arid pastoral system in the Northern Cape Province, South Africa. The Succulent Karoo Biome, of which Leliefontein is part, is a semi-arid area with low winter rainfall and it consists of unique flora with many endemic species. This biome is rated as one of only two semi-arid regions to qualify as a globally significant biodiversity hotspot of plant and animal diversity (Todd and Hoffman, 2009) and is ranked among 27 global biodiversity hotspots (Myers et al., 2000).

The Leliefontein communal area which is one of the six former coloured rural areas of Namaqualand in South Africa was established in 1816 when it originated as a mission station of the Wesleyan Methodist Missionary Society. Leliefontein communal area is roughly 192 000 ha in size and comprises of 10 villages (Samuels, 2013). About 1500 households are spread across the 10 villages (Allsopp et al., 2007).

The main land use in Leliefontein communal area is extensive livestock farming. Livestock (goats and sheep) are kept at temporary and permanent stockpots that are scattered around the

rangeland (Samuels et al., 2013). The vegetation in Leliefontein is composed of Succulent Karoo, Mountain Renosterveld and Mountain Fynbos shrublands (Helme and Desmet, 2006). This study focussed on Renosterveld vegetation which has a high species richness of geophytic plants and has one of the highest stocking densities in the communal area (Samuels, 2013).

1.8 Research problem

For centuries, the main land use in Leliefontein has been livestock grazing, but there is a general lack of information about the chemical composition of forages in terms of nutritional components. To date, there is no documented study on the effect of anti-nutritional and nutritional components on the quality of forage plants in this area. As a result there is lake of reliable information for sustainable management of the range resources to boost livestock production.

1.9 Objectives of study

This study aimed to achieve the following objectives:

- To compare and contrast the quality and nutritive values of Renosterveld forage plant types of Leliefontein during dry and wet seasons;
- To compare and contrast the secondary compounds of forage plants in Leliefontein during the dry and wet seasons; and
- To understand how plant nutrients and secondary compounds may influence forage quality in a semi-arid rangeland.

1.10 Research questions

The principal question of the study was:

How does forage quality amongst Renosterveld growth forms differ between the wet and dry periods in Namaqualand?

1.10.1 Research sub-questions:

- (1) Are there variations in nutritional value between different forage growth forms within and between two seasons?
- (2) Are there variations in secondary compounds between different forage growth forms within and between two seasons?
- (3) Is there a relationship between plant chemical defences and forage nutrition in Renosterveld vegetation?

1.11 Significance of the study

This study analysed different types of forage growth forms (grasses, reeds, non-succulents, herbs, leaf succulents, stem succulents and trees) that are widespread in the study area, in order to understand the main reasons behind the preference of animals when livestock feed on plants and avoid eating other plants within the same rangeland. In addition, the study could provide valuable insights into future rangeland management in the Leliefontein area which could include grazing management plans and regulations. This type of study also contributes new knowledge and enhances understanding for assessing the quality of forage plants in semi-arid pastoral rangelands.

CHAPTER TWO

STUDY AREA

2.1 Introduction

In this chapter, the biophysical, namely, the geographical location, climate and soils, and sociopolitico-economic environments of the Leliefontein communal area are described.

2.2 Geographical location

Leliefontein is one of six areas in Namaqualand formerly known as 'coloured' reserves; the others are Steinkopf, Komaggas, Concordia, Pella and the Richtersveld (Figure 2.1) (Wisborg and Rohde, 2005; Kelso, 2010; Samuels, 2013). This study was conducted in Leliefontein village, which constitutes a part of the Leliefontein communal area and lies in a west-east band extending across the Kamiesberg mountain range with altitudes of roughly 1 300 m above sea level (Anderson, 2008).

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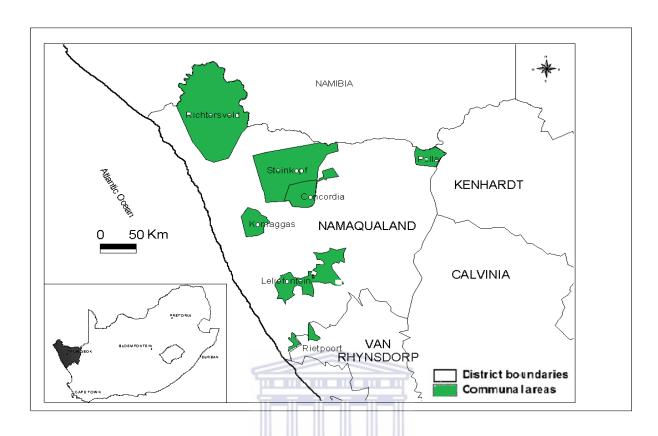


Figure 2.1: The communal areas in Namaqualand. The study was conducted in and around the Leliefontein Communal area, adapted from (Anderson et al., 2010).

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The Leliefontein communal area which is about 192 000 ha in size contains 10 villages (Figure 2.2), of which the village of Leliefontein is the oldest and most central. The Leliefontein communal area is surrounded by 84 farms; these farms are divided into 77 privately owned farms and seven communal farms that are owned by the local municipality (Samuels 2013).

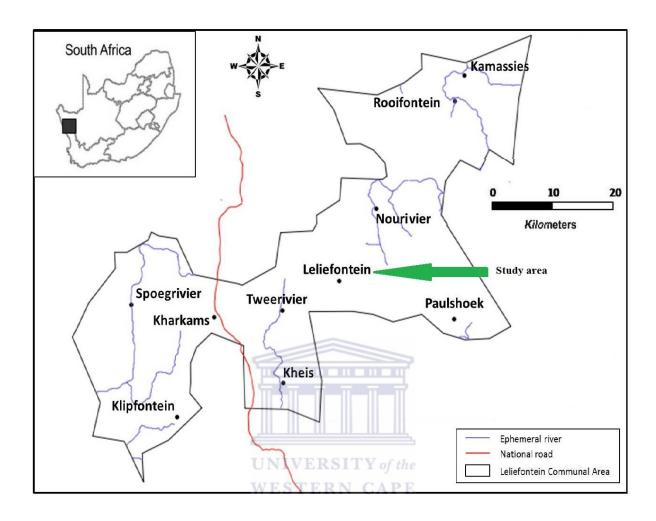


Figure 2.2: The location of the Leliefontein village, which mediates the tenth villages in communal area, adapted from (Samuels et al., 2008).

2.3. Climate of Leliefontein

Leliefontein is a semi-arid region with a Mediterranean-type climate with warm, dry summers and cold, wet winters. During the summer season (December to February), temperatures in the Leliefontein communal area may reach a maximum of 40 °C (Samuels et al., 2008) and in the winter season (May to August), minimum temperature may drop below 0 °C (Anderson, 2008; Desmet, 2007). In the Leliefontein village, the seasonal temperatures change fairly uniformly

with an average maximum in summer of 35 °C and an average winter minimum of 2°C (Anderson, 2008). In addition, the mean annual rainfall is 392 mm since 1885 (Samuels, 2013).

The rainfall season is mainly in winter and is brought by cold fronts from across the Atlantic Ocean, which may also carry snow. Summer rainfall occurs as one move towards the east (Desmet, 2007). Furthermore, heavy dew and the incidence of fog in the west coast areas occur during the winter because of the cold Atlantic Ocean (Desmet, 2007).

2.4. Soils of Leliefontein

Soils of the upland areas in Kamiesberg are shallow and red sandy on Dorbank, especially in the flat lands between the mountain ridges (Francis et al., 2007). Soils in the study area are consistent, and originated from the fundamental granites and gneisses that form such prominent attributes in the landscape. Usually the convex slopes are very rocky with shallow, often coarsegrained (Helme and Desmet, 2006), and yellow brown to brown loamy sand (Mucina and Rutherford, 2006). The continual cultivation of soils on the flatlands have, however, led to the loss of soil nutrients (Allsopp, 1999; Samuels, 2013).

Types of soils have a significant impact on the vegetation types which arise in the area and lead to a varied range of soil conditions ideal for plant growth (Anderson and Hoffman, 2007; Desmet, 2007). The vegetation composition is determined by the composition and depth of soil (Van Wyk and Smith, 2001). Distribution of biodiversity is affected by the physical and chemical properties of soils (Bronick and Lal, 2005).

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2.5. Vegetation

The Leliefontein area is situated in the desert of Namaqualand in the Succulent Karoo biome, a biodiversity hotspot of global significance that supports the world's richest succulent vegetation (Kelso, 2010), and forms one of 27 internationally recognised biodiversity hotspots (Myers et al., 2000). This is due to great concentrations of endemic taxa, including 150 vascular plant species

(Van Wyk and Smith, 2001). The Kamiesberg is host to large numbers of different vegetation types and is itself an area of high biodiversity (Anderson et al., 2010).

Mucina and Rutherford (2006) stated that there are six main vegetation types in the Leliefontein communal areas, namely, Namaqualand Heuweltjieveld, Kamiesberg Granite Fynbos, Namaqualand Klipkoppe Shrubland, Kamiesberg Mountains Shrubland, Namaqualand Blomveld and Namaqualand Granite Renosterveld. In addition, there are three smaller vegetation types covering less than 2% of the area: Namaqualand Inland Duneveld, Namaqualand Rivier and Namaqualand Sand Fynbos (Figure 2.3), (Samuels, 2013). Namaqualand Klipkoppe Shrubland covers about 52% of the communal area. Although Namaqualand Granite Renosterveld only makes up 6.8% of the communal area, it is about 65% of the total vegetation found around Leliefontein village (Figure 2.3) (Samuels, 2013).

Namaqualand Granite Renosterveld was the focus of this study, which is the most abundant and accessible vegetation type for the pastoralists in Leliefontein village. Namaqualand Granite Renosterveld is characterised by large stands of the woody shrub *Dicerothamnus rhinocerotis* and the grass species *Merxmuellera stricta* (Anderson et al., 2010). Renosterveld is known for its high diversity of geophytes which contain monocots such as *Asparagaceae*, *Amaryllidaceae*, *Hyacinthaceae*, *Iridaceae*, *Orchidaceae* as well as dicots such as *Oxalidaceae* and *Geraniaceae* (Forbes, 2014).

This type of vegetation occurs on the upper plateaus of the Kamiesberg (at 1000 – 1300 m), and is typically found in the flat, deeper soils of the plateaus (Helme and Desmet, 2006). Renosterveld is affected by conversion in the Kamiesberg. More than 20% of this vegetation type has been transformed through agriculture and only 5% lost through cultivation which includes cropping and grazing. This vegetation type supports the second highest number of endemic plant species in the Kamiesberg (Helme and Desmet, 2006).

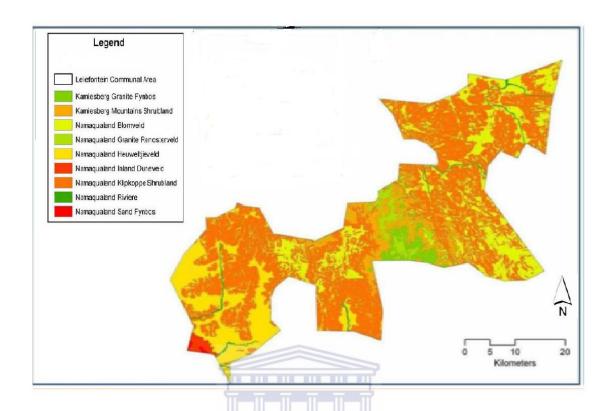


Figure 2.3: Vegetation map of the nine different vegetation types occurring within the Leliefontein communal area (adapted from Samuels (2013)).

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2.6. Land use

In general, the dominant land use in the Succulent Karoo biome is extensive livestock farming with sheep and goats (Jonas 2004; Todd and Hoffman, 2009). The land use that has had a negative impact on the vegetation of the Succulent Karoo is mining. However, it does not occur in the Leliefontein communal area. The main land use in Leliefontein communal area is extensive livestock farming (Samuels et al., 2008). Leliefontein village has about 30 small stock herds with about 5 000 goats and sheep. In addition, firewood harvesting and medicinal plant collection are other land use activities in the communal area. Moreover, on the flatter, deeper soils of valley bottoms, dry land cropping is practised (Samuels, 2013). People in Leliefontein generally rely on livestock as a resource for generating cash and also as a means of investment in times of economic hardship (Debeaudoin, 2001).

In semi-arid areas the most important features of an intact wetland system is its ability to absorb

rainfall, store and release it slowly to control water flow. The Kamiesberg is blessed with a great number of seasonal wetlands and streams (Helme and Desmet, 2006). Wetlands in the Kamiesberg have several species that are palatable to livestock (Malan et al., 2010). In the Leliefontein village, pastoralists move their herds between several ephemeral wetlands for grazing to provide their animals with good quality forage during summer as these areas hold water longer into the dry season for livestock to drink. Grazing is concentrated around the villages and there are no internal fences between village commons to restrict livestock (Samuels, 2013; Samuels et al., 2015).

2.7. People in Leliefontein

The Namaqualand area was populated mainly by Nama Khoikhoi pastoralists and huntergatherer San before 1700 (Hoffman and Rohde, 2007; Kelso, 2010). Presently, the majority of people in Leliefontein are of mixed ancestry. They are descended from the original Nama people and European settlers (Debeauoin, 2001) with Afrikaans as their home language (Hoffman and Rohde, 2007; Hongslo et al., 2009). In 2001, the census of the population for the Leliefontein communal area was 7 571 people in 1 399 households in the region (Atkinson and Ravenscroft, 2002). According to the Northern Cape Department of Agriculture, the average size household is estimated at six people. From 1960 to 1997, the Leliefontein village showed a fivefold increase in the number of households (Kelso, 2010).

2.8. Pastoral system in Leliefontein village

The pastoral system in Leliefontein area is characterised by seasonal altitudinal movements between the lowlands and the uplands (Todd and Hoffman, 2000). Herders manage numbers of livestock in a communal area and have evolved several herding strategies in response to environmental drivers (Samuels et al., 2007; Samuels, 2013). Herds of small stock, which include sheep and goats, are grouped at stock posts scattered around the rangeland (Samuels, 2013). In Leliefontein, communal area croplands comprise 12% of the total area, and barley, rye, oats and lucerne are the major cultivated crops grown during winter. These crops are also used as

fodder for livestock during the dry summer periods when the rangeland is in a poor condition. Herds usually return to these summer locations after the harvesting of crops to graze on crop residues (Bennett et al., 2007; Samuels, 2013). Heavy grazing in communal areas has affected the vegetation composition and diversity by increasing the richness of unpalatable species (Todd and Hoffman, 2009; Al-Rowaily et al., 2012; Bösing et al., 2014). In addition, it has resulted in a decrease of perennial, palatable shrub species cover (Bösing et al., 2014).



CHAPTER THREE

Characterising the Nutritional Value of Forage for Livestock in a Semi-Arid Shrubland in Namaqualand

3.1 Abstract

Forage quality in terms of nutritional values is affected by several factors such as vegetation stages, plant species and grazing intensity. Therefore, assessing the nutritive values of available forages is important to develop appropriate grazing management plans. This study focused on the nutritive values of the forage material, particularly sodium (Na), calcium (Ca), magnesium (Mg), potassium (K), phosphorus (P), nitrogen (N), crude protein (CP), neutral detergent fibre (NDF), acid detergent fibre (ADF), dry matter digestibility (DMD), metabolizable energy (ME), dry matter intake (DMI) and relative forage value (RFV) to investigate how nutritional values differ between forage growth forms, and between the wet and dry seasons. The findings showed that the assessed forage growth forms had different nutritive values and that the forage quality of the various types of plants in the Leliefontein village was not significantly different between the different seasons, but the forage quality of the different forage types was significantly different from each other within a season. Leaf Succulents (LS) had a higher nutritive value compared to other growth forms. Mineral nutrient concentrations of the different forage types were generally sufficient to satisfy the requirements of small ruminants. However, in certain forage types, Na and P concentrations were below the critical levels required by goats and sheep.

Keywords: nutritional, forage, quality, nutritive value, minerals, Leliefontein.

3.2 Introduction

Plants constitute the main source of nutrients to livestock in extensive grazing systems (Njidda, 2010). Natural rangelands provide feed to a large number of livestock and are considered one of the cheapest sources of forages for grazing animals (Ismail et al., 2014). For this reason, some countries, specifically developing countries, depend on their natural rangelands to sustain their livestock industry. Livestock living under rangeland conditions are generally exposed to a range of forage types which are highly variable in their nutritional quality (Njidda, 2010). However, natural rangelands are complicated systems that differ from each other as they are characterised by their exclusive combination of different plants. This difference causes significant variation in forage quality because of the differences between periods of seasons and areas (Allison, 1985; Pinkerton and Cross, 1991; Pinkerton, 2005; Amiri and Mohamed Shariff, 2012).

In natural rangelands, the nutritional value of the forages is variable and collectively based on some effects that are associated with environmental factors such as soil type, the availability of water, climate, altitude (Todorova et al., 2002; Amiri and Mohamed Shariff, 2012) and management practices (Čop et al., 2009; Amiri and Mohamed Shariff, 2012). Deficiency of nutritious forages is one of the major problems facing livestock production in these rangeland conditions. Cook and Stubbendieck (1986), for example, reported that the differences of nutritional content of forage plants species may be because of an inherent ability to extract certain nutrients from the soil and to concentrate them in tissues.

Assessing the nutritional value of rangelands is mostly associated with providing energy, protein and minerals for the animals. According to Arzani et al. (2006), the chemical analysis of forage plants works as a comparative measure of the differences between species and changes with season. Therefore, the determination of essential nutrients and the evaluation of the chemical composition of these forages, which are required for optimal growth of livestock, are fundamental factors in addressing this problem. These essential nutrients are composed of water, carbohydrates, proteins, minerals and vitamins (Aberoumand and Deokule, 2009; Gomez, 2011). Factors that determine the required quantities of these nutrients are the animals' growth stages, production, reproduction, lactation, growth and activity (Cunha and Macdowell, 2012). On the other hand, factors that influence the nutrient equilibrium of animals include the nutrient requirements of the animals as well as the nutrient content, quantity and digestibility of the

consumed forages. In addition, forage quality and its nutritional value are influenced by a number of factors such as the stages of vegetation maturity, plant species and grazing intensity (Kaplan et al., 2014). Thus, the performance of the animals in the grazing season depends on the quality of the available forage and its nutrient content.

Livestock keepers must be familiar with the nutritional dynamics of forages in order to achieve sustainable growth and reproduction of their animals (Ganskopp and Bohnert, 2003). It is important for livestock keepers to be aware of rangeland quality changes between seasons (Corson et al., 1999) and to have a proper understanding of forage quality dynamics in rangelands. This will help livestock keepers to make appropriate decisions when selecting forages and supplements in line with the needs of the animals (Teka et al., 2012) that will eventually lead to optimum livestock performance. Key aspects to consider when evaluating such forages include the protein, fibre and mineral nutrient concentrations of the forage plants. In the study area in Leliefontein, no documented information was available on the nutritive values of different forages in relation to different seasons. Therefore, it was necessary to evaluate the nutritive value during the wet and dry seasons in relation to the animals' requirements.

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3.3 Aim of the study

The main aim of this study was to assess the nutritional quality of the available forage plants in Renosterveld vegetation in the Leliefontein rangeland and to investigate how the nutritional values might differ between plant growth forms and seasons. The research questions are as follows:

- How does the mineral content differ between different growth forms within and between different seasons in Renosterveld vegetation?
- How does the crude protein concentration differ between the forage growth forms in Renosterveld vegetation?
- How does forage quality in terms of growth forms and season affect digestibility?

3.4 Material and methods

3.4.1 Study site

The study was conducted in the Kamiesberg uplands of the Leliefontein communal area (LCA) (30° 18′ 51′'S, 18° 10 04′ 58′' E) which is situated in the semi-arid Namaqualand region of South Africa. The LCA is approximately 1 920 km² in extent. The maximum temperature in the Leliefontein communal area may surpass 40 °C and minimum temperatures during the winter season (May to August) often fall below freezing point in the upland areas (Desmet, 2007; Samuels, 2013). Rainfall occurs mainly during winter, but thunderstorms during summer are not uncommon.

This study focused on the Namaqualand Granite Renosterveld vegetation type which is considered part of the Fynbos Biome (Mucina and Rutherford, 2006). Renosterveld is a shrubland that is dominated by *Elytropappus rhinocerotis* (renosterbos), a 1.0-1.5m tall, unpalatable woody shrub. This vegetation type contains the second highest number of endemic plants (mainly geophytes) in the Kamiesberg region (Helme and Desmet, 2006). A full description of the study area is provided in Chapter Two.

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3.4.2. Sample collection and preparation

Plant species that were collected corresponded to the plants grazed and not grazed during a diet selection study conducted by Samuels et al. (2015). Plant parts collected included only the parts that have the potential to be consumed by livestock (i.e. sheep, goats, donkeys and cattle). These parts included leaves, green twigs and flowers. Flowers were mainly from geophytes that were flowering at the time of sampling. Approximately two hundred plant species were collected. These are all the species that were encountered in the field and comprised of grasses, reeds, herbs, non-succulents, leaf succulents and trees.

Wet season sampling took place from September to October 2012 and completed during May to September 2013. Wet season sampling occurred over two seasons as logistical reasons prevented sampling to be completed in one year. During the dry season, plants were collected during March 2013. Not all plant species were available in the rangeland during the dry season that was

available during the wet season. No flower parts were collected during the dry season as no plants were in flower. During the wet season, biomass from a particular plant species was collected from at least seven individuals from each species and placed together in a brown paper bag and placed in an oven at 60°C to dry. Plant samples were left in the oven until they were completely dry. Dry mass was taken after 72 hours, and when no changes in mass were recorded the next day, the samples were considered dry. Dry samples were milled using a Wiley mill. Corresponding voucher specimens were also collected from each plant species and later identified in the laboratory. Plants were thereafter grouped into their respective growth forms: in the wet season grasses (seven species), herbs (eight species), leaf succulents (eight species), nonsucculents (79 species), reeds (three species), trees (six species) and stem succulents (two species) and in the dry season grasses (eight species), herbs (seven species), leaf succulents (nine species), non-succulents (55 species), reeds (four species), trees (two species) and stem succulents (no species) for statistical analyses.

3.4.3 Chemical analyses

3.4.3.1 Mineral elements and crude protein determination

A 0.4 g sample of the dry, milled plant material was digested in 5 ml of sulphuric-peroxide digestion mixture in a heating block, as described by Moore and Chapman (1986). After digestion, the samples were allowed to cool to room temperature after which they were filtered through Whatman No 1 filter paper into a 100 ml volumetric flask and diluted to volume with distilled water (dH₂O). After dilution, the samples were stored for further analyses. The digested samples were later analysed for K, Ca, Mg and Na concentrations using a UnicamPyeSolaar (Mseries) Atomic Absorption Spectrophotometer (AAS) (Unicam Unlimited, Cambridge, UK). Phosphorus concentrations were determined using a Spectroquant ® Pharo 300-M unit (Merc (Pty) Ltd.) according to the distributor's specifications. Total nitrogen concentrations were determined by the Kjeldahl method (Moore and Chapman, 1986) using a Büchi Nitrogen Distillation Unit model K-300 (Labotec, Büchi Switzerland). The nitrogen content (%) obtained was multiplied by a factor of 6.25 to obtain the percentage crude protein (BüchiLabotec).

3.4.3.2 Fibre content and nutritional quality

Neutral detergent fibre (NDF) and acid detergent fibre (ADF) were determined using the ANKOM 200/220 Fibre Analyser in accordance with the operating instructions. Neutral detergent fibre and ADF values obtained were used to calculate DMD, DMI (Undersander et al., 1993; Schroeder, 2009; Amiri and Mohamed Shariff, 2012), ME (Belyea et al., 1993; Amiri and Mohamed Shariff, 2012) and relative feed/forage value (RFV) (Newman et al., 2009; Schroeder, 2009) using equations 1- 4:

- **1.** Dry matter digestibility was calculated from % ADF. % DMD= $88.9 (ADF\% \times 0.779)$ (Undersander et al., 1993).
- **2.** Metabolizable energy where ME/DM is the metabolizable energy in mega joules (MJ) per kg of feed DM (MJ/kg DM) (ME) = 0.17% DMD 2.0 (Belyea et al., 1993).
- **3.** Dry matter intake (DMI) is an estimate of the relative amount of forage an animal will eat when only forage is fed. Dry matter intake as a percent (DMI): % DMI= 120 ÷ % NDF (Undersander et al., 1993).
- **4.** Relative feed value (RFV): RFV= (%DMD x %DMI) ÷ 1.29

3.4.4 Statistical analyses

The Statistical Package for the Social Sciences Version 22 (SPSS Inc., Chicago, IL) was used to test the data for normality using a Shapiro-Willks test. Where necessary, the data were log-transformed to achieve normality after which a one-way Analysis of Variance (ANOVA) was performed to determine whether significant differences were found between the plant growth forms within a season and whether the same growth forms differed between sampling seasons. Where significant differences were observed, a least significant difference (LSD) post hoc test was performed to determine between which growth forms or seasons these differences occurred. Where normality could not be achieved, statistical analyses were performed using Kruskal-Wallis analysis. A principal component analysis (PCA) was used to examine forage quality of the species based on the information provided from the results.

3.5 Results

3.5.1 How does the mineral content differ between the growth forms and season in Renosterveld vegetation?

3.5.1.1 Differences in growth form

Significant differences were observed in Mg concentrations in both wet $(F_{(6,108)}=10.482$, p<0.001), and dry $(F_{(5,82)}=8.045,$ p<0.001) seasons between the different forage types (Figure 3.1**A** and **B**). Significant differences were found in Mg concentrations between leaf succulents in the wet as well as in the dry seasons and other growth forms except trees. Significant differences were found in Ca concentrations in both the wet (Figure 3.1**C**, $H_{(6,109)}=22.127$, p=0.001) and dry seasons (Figure 3.1**D**, $F_{(5,82)}=6.340$, p<0.001) among the different forage types. Significant differences in Ca were found between leaf succulents and other growth forms except trees in both the wet and dry seasons.

There were no significant differences (p>0.05) in K concentrations between the different types of forage plants in the wet season (Figure 3.1E). However, significant differences between leaf succulents and other growth forms except trees ($F_{(5,82)}$ =2.615, p=0.031) were found in the dry season (Figure 3.1F).

There were significant differences in Na concentrations between the different forage types in the wet season (Figure 3.1.G, $H_{(6,109)}$ =14.246, p=0.027) in leaf succulents compared to reeds, grasses and non-succulent shrubs. Nevertheless, there were no significant differences (p \geq 0.05) between forage growth forms in the dry season (Figure 3.1H).

There were only significant differences in P concentrations of forage growth forms in the wet season (Figure 3.1.**I**, $F_{(6,108)}$ =3.009, p=0.009) between grasses and herbs. No significant differences (p \ge 0.05) in P concentrations were found among forage growth forms in the dry season (Figure 3.1.**J**).

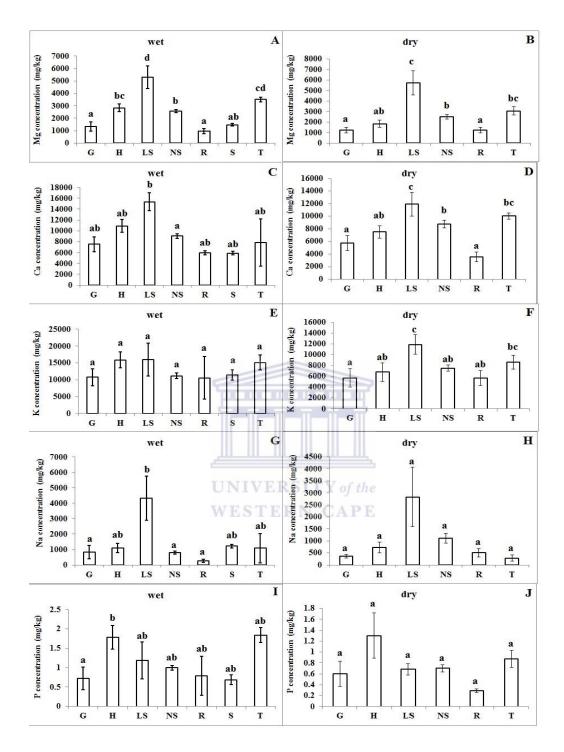


Figure 3.1: Mean mineral nutrient concentrations (\pm SE) of forage plants within wet and dry seasons in the Leliefontein communal area. Significant differences (p<0.05) are indicated by different letters above the bars between different forage growth forms in each season. G: grasses; H: herbs; LS: leaf succulents; NS: non-succulents; R: reeds; S: succulents and T: trees.

3.5.1.2 The effect of season

There were not significant differences (p>0.05) for Na, Ca and Mg concentrations between the two seasons in nutrient concentrations of each of the forage growth forms (Figure 3.2.A, 3.2.B, 3.2.C). Potassium concentrations showed significant differences between the two seasons in herbs ($F_{(1,14)}$ =6.506, p=0.024), non-succulent shrubs ($F_{(1,133)}$ =0.823, p=0.001), and trees ($F_{(1,7)}$ =6.394, p=0.045), but there were no significant (p>0.05) differences between the wet and dry seasons in K concentrations for leaf succulents, grasses and reeds (Figure 3.2.**D**). Furthermore, the P concentrations for non-succulent shrubs and trees showed significant differences ($H_{(1,134)}$ =10.473, p=0.001) and ($F_{(1,7)}$ =10.132, p=0.019) between the wet and dry seasons (Figure 3.2.**E**).



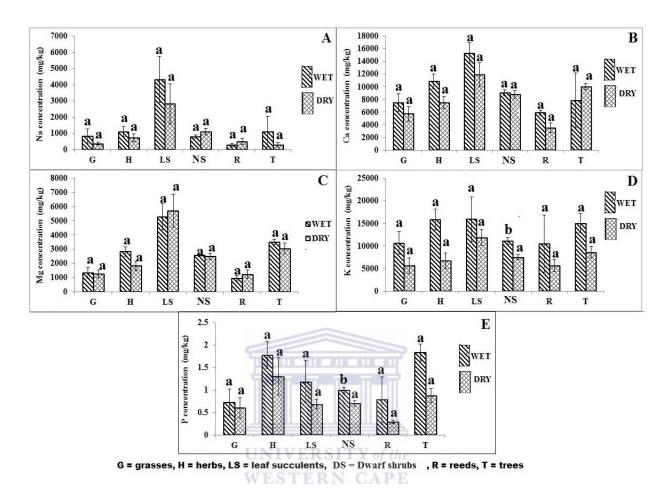


Figure 3.2: Mean mineral nutrient concentrations (±SE) of forage plants between wet and dry seasons. Significant differences (p<0.05) are indicated by different letters above the bars between different forage growth forms in each season. G: grasses; H: herbs; LS: leaf succulents; NS: non-succulents; R: reeds; S: succulents and T: trees.

3.5.2 How does the crude protein concentration differ between the forage growth forms and season of Renosterveld vegetation?

The results showed significant differences in the amount of crude protein (CP) content in the wet season ($F_{(6,108)}$ =3.784, p=0.002) and in the dry season ($F_{(5,82)}$ = 5.003, p=0.001) amongst the different growth forms (Figure 3.3.A, 3.3.B). Between the two seasons, significant differences in crude protein concentration were found in non-succulent shrubs ($F_{(1,133)}$ =12.157, p=0.001), reeds

 $(H_{(1,7)}=4.500, p=0.034)$ and trees $(F_{(1,7)}=33.966, p=0.001)$. During the dry season, crude protein concentrations were significantly lower. No significant differences $(p\geq0.05)$ were observed in the other growth types (grasses, herbs and leaf succulents) between the two seasons (Figure 3.4).

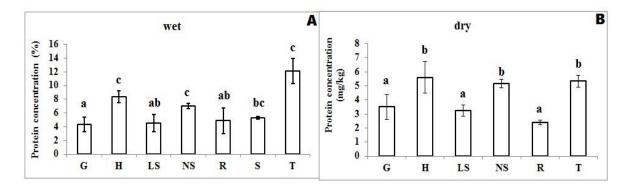


Figure 3.3: Mean crude protein concentrations (±SE) of forage plants within wet and dry seasons. Significant differences (p<0.05) are indicated by different letters above the bars between different forage growth forms in each season. G: grasses; H: herbs; LS: leaf succulents; NS: non-succulents; R: reeds; S: succulents and T: trees.

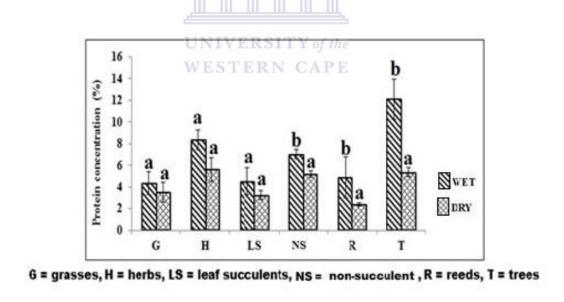


Figure 3.4: Mean Protein concentrations (\pm SE) of forage plants between wet and dry seasons in the Leliefontein communal area. Significant differences (p<0.05) are indicated by different

letters above the bars between different forage growth forms in each season. G: grasses; H: herbs; LS: leaf succulents; NS: non-succulents; R: reeds; S: succulents and T: trees.

3.5.3. How does digestibility differ in terms of growth form and season?

3.5.3.1 Difference between growth forms

Significant differences were observed in NDF concentrations in the wet season (Figure 3.5A, $F_{(6,112)}$ =5.469, p<0.001) with NDF concentrations in leaf succulents being significantly lower (p<0.05) than the other growth forms. In the dry season, NDF concentrations differed significantly between the growth forms (Figure 3.5B, $F_{(5,83)}$ =4.761, p=0.001) with leaf succulents and trees significantly lower (P<0.05) than the other growth forms.

Acid detergent fibre concentrations were significantly different in the wet season (Figure 3.5C, $F_{(6,112)}=10.647$, p<0.001) and in the dry season ADF) (Figure 3.5D, $F_{(5,83)}=10.393$, p<0.001) between the different growth forms. Leaf succulents and trees showed significantly lower concentrations (p<0.05) compared to the other growth forms.

Hemicellulose concentrations differed significantly in the wet season (Figure 3.5**E**, $F_{(6,112)}$ =7.810, p<0.001) and in the dry season (Figure 3.5**F**, $F_{(5,83)}$ =16.382, p<0.001) between the different growth forms.

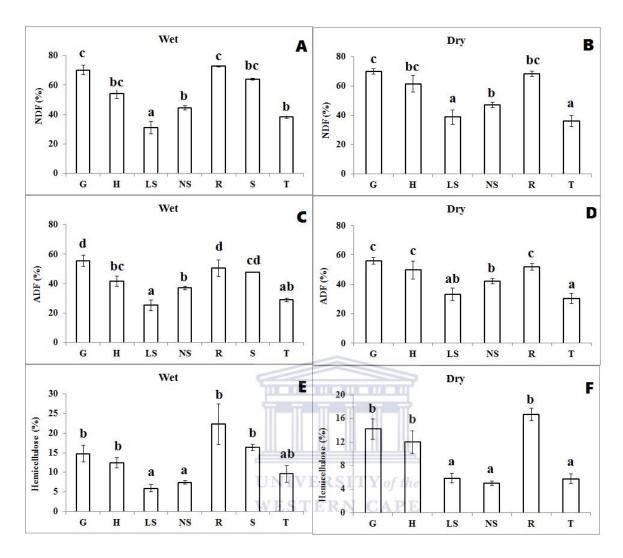


Figure 3.5: Mean NDF, ADF and hemicellulose concentrations (\pm SE) of forage plants within wet and dry seasons. Significant differences (p<0.05) are indicated by different letters above the bars between different forage growth forms in each season. G: grasses; H: herbs; LS: leaf succulents; NS: non-succulents; R: reeds; S: succulents and T: trees.

Significant differences were observed in the concentration of dry matter digestibility (DMD) in the wet season (Figure 3.6**A**, $F_{(6,112)}$ =5.469, p<0.001) and in the dry season (Figure 3.6**B**, $F_{(5,83)}$ =4.761, p<0.001) between forage growth forms.

In the wet season, the metabolizable energy (ME) of forage growth forms showed significant differences between the growth forms (Figure 3.6C, $F_{(6,112)}$ =5.469, p<0.001). Metabolizable

energy in the dry season also showed a significant difference between grasses and non-succulents (Figure 3.6**D**, $F_{(5.83)}$ =4.761, p<0.001). Significant differences between leaf succulents, non-succulent shrubs, herbs, stem succulents reeds and grasses (Figure 3.6**E**, $F_{(6.112)}$ =8.407 p<0.001) were observed in the wet season. Dry matter intake (DMI) in the dry season differed significantly (Figure 3.6**F**, $F_{(5.83)}$ =7.393, p<0.001) between leaf succulents, non-succulents, herbs, reeds and grasses, while there were no significant differences (p≥0.05) between herbs, reeds and grasses in the dry season (Figure 3.6**F**).

However, relative forage values (RFV) in the wet season showed significant differences (Figure 3.6**G**, $F_{(6,112)}$ =7.684, p<0.001) between growth forms .Relative forage values (RFV) in the dry season were significantly different (Figure 3.6**H**, $F_{(5,83)}$ =6.613, p<0.001) between non-succulents, reeds and grasses.



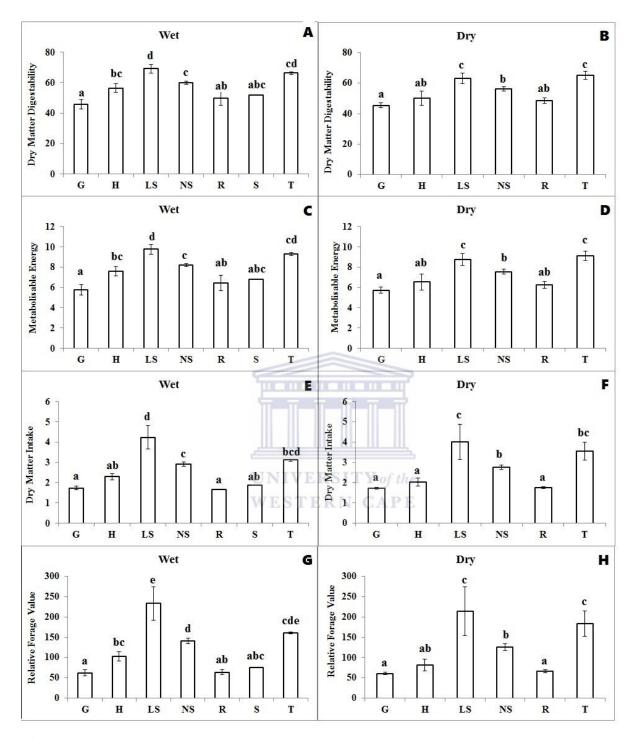


Figure 3.6: Mean DMD, ME, DMI, RFV concentrations of (\pm SE) of forage plants within wet and dry seasons. Significant differences (p<0.05) are indicated by different letters above the bars between different forage growth forms in each season. G: grasses; H: herbs; LS: leaf succulents; NS: non-succulents; R: reeds; S: succulents and T: trees.

3.5.3.2 Effect of season

Between seasons, the results showed there were no significant differences in NDF and ADF concentrations of forage growth forms ($p\ge0.05$) between the two seasons (Figure 3.7A, 3.7B). Hemicellulose values of forage growth forms showed no significant differences ($p\ge0.05$) between seasons except in non-succulents (Figure 3.7C). Based on dry matter digestibility (DMD) and the metabolizable energy (ME) of growth forms of forages, no significant differences were observed between the two seasons ($p\ge0.05$), except in non-succulents which showed a significant difference (p<0.05) between the wet and dry season (Figure 3.7D, Figure 3.7E) There were no significant differences in relative forage values of growth forms ($p\ge0.05$) between the seasons (Figure 3.7G).



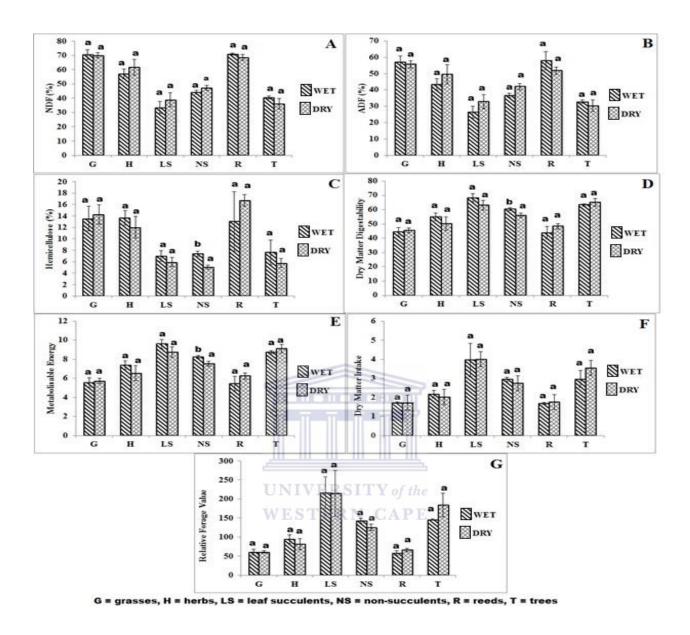


Figure 3.7: Mean NDF, ADF, hemicellulose, DMD, ME, DMI and RFV concentrations (±SE) of forage plants between wet and dry seasons. Significant differences (p<0.05) are indicated by different letters above the bars between different forage growth forms in each season. G: grasses; H: herbs; LS: leaf succulents; NS: non-succulents; R: reeds; S: succulents and T: trees.

3.5.4 Understanding plant forage quality considering all nutritional factors

Eigenvalues of axes I and 2 were 55.33% and 13.75% respectively, explaining 69.08 of the total variability. According to Figure 3.8, non-succulents are randomly distributed, which means that they cannot be particularly associated with any of the other groups. Grasses, irrespective of season could be associated with high fibre and hemicellulose contents whereas most succulent species had relatively high forage values. Individual plant species possessing high forage quality were *Carpobrotus* (LS), *Cotula barbarta* (H) and *Tetabromus* (G). Tree species showed good forage quality in terms of crude protein.

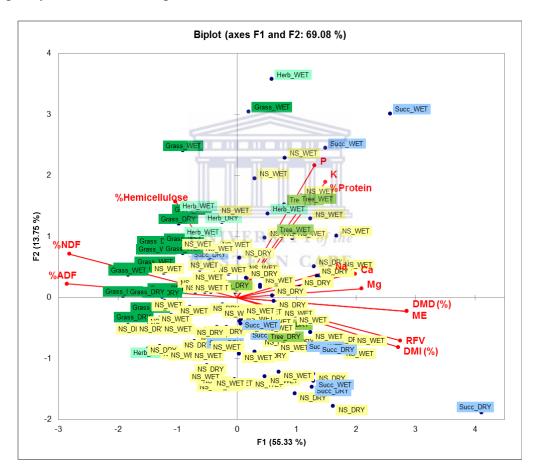


Figure 3.8: Principal component analysis biplot of the variables measured during the study (F1) and plant growth forms (F2). The percentage of total variance explained by each PC (first PC: 55.33 %; second PC: 13.75 %).

3.6 Discussion

3.6.1 How do mineral concentrations differ between growth forms of forage plants at different seasons in Renosterveld vegetation?

Leaf succulents exhibited highe values of most minerals tested in both wet and dry seasons which indicate good nutritional quality compared to other growth forms. Furthermore, the reason for high mineral concentrations in leaf succulents could be because the leaf tissue of succulent plants have the ability to store water and accumulate organic acids required to support their physiological function when external water is not available (Nalawde and Bhalerao, 2015) which could act as an adaptation to drought conditions (Ogburn and Edwards, 2012).

Cook and Stubbendieck (1986) also reported that the differences of chemical content of forage plants species may be because of an inherent ability to extract certain nutrients from the soil and to concentrate them in their tissues. In addition, soil properties such as soil pH may also influence the mineral concentration of rangelands (Snyman, 2003). Plants absorb minerals from the soil solution and incorporate them into their tissues as they grow. Therefore, the ability of plants to obtain both water and mineral nutrients from the soil is related to their capacity to develop extensive root systems which differ among plant types (López-Bucio et al., 2003; Marschner, 2011). Since there is significant spatial and temporal variability in plant species distribution, it could be argued that soils also play a major role in the nutrient contents of Renosterveld plant species. The differences in the rate of absorption of nutrients between plant types could also be a reason for the variation in mineral concentrations of different forage growth forms in this study (Barber, 1995).

Previous studies have also shown differences in the nutritive values of forage plants between different seasons. These include Scogings et al. (2015) who showed that there are variations in N and P concentrations of forage plants between seasons in a semi-arid savannah in South Africa. Similarly, Ophof et al. (2013) in Northern Finland found that seasonal variations affect the quality and availability of reindeer forage plant species as well as various dwarf shrub species. Furthermore, Teka et al. (2012) in semi-arid areas of Borana, Ethiopia reported that seasonal variation has a significant influence on the nutritional quality of key herbaceous species in the region, and Ganskopp and Bohnert (2003), and Hussain and Durrani (2008) relate that the

mineral composition of grasses changed seasonally in Pakistan. The present study found that the concentrations of minerals of most types of growth forms in the Leliefontein communal rangeland were not significantly different between seasons. The reasons for similarity no in nutritive values between seasons in Leliefontein is unclear, but it could be because livestock are grazing in the rangeland during the dry and wet seasons, and there is an increase in plant growth through animal wastes, which are deposited and recycled in the field as a source for high nutrients (Tilman et al., 2002; Samuels et al., 2015).

3.6.2 How do the crude protein concentrations differ between the forage growth forms and seaons in Renosterveld vegetation?

Amongst the growth forms of plants in the present study, trees, non-succulents and herbs showed high Crude Protein (CP) concentrations, while CP was low in grasses and reeds. The researchers of previous studies conducted in the semi-arid region of northern Egypt, Salem et al. (2006); in the Chaharmahal Bakhtiary Province of Iran, Arzani et al. (2006); in the north-eastern part of Nigeria, Njidda and Nasiru, (2010); in the CautoValley in Cuba (Juárez et al., 2013); and in South Darfur in Sudan Ismail et al. (2014) have all reported higher amount of protein in different forage plants than in the present study in general. These variances among different forage types could be due to differences in soil types and the nutrient status of soil (Teka et al., 2012). It may also be attributed to the age and maturity of forage plants when they are collected. At early growth stages of forage plants, leaves contain high protein concentrations and are low in fibre (Fatur and Khadiga, 2007). Moreover, the differences in CP concentrations between these forages are perhaps due to differences in the accumulation of proteins in these forage plants during different seasons (Salem et al., 2006).

3.6.3 How does forage quality in terms of growth form and season affect digestibility?

Grasses and reeds showed higher NDF and ADF concentrations than other forages. Higher ADF content of grasses and reeds could be associated with higher concentrations of fibrous tissues. Grasses have a greater quantity of stems (Amiri and Mohamed Shariff, 2012) which result in more fibrous tissues as opposed to other forage types. The high amount of NDF within grasses

were relatively close to the results reported by Burns et al. (1997), Vendramini (2010), and Amiri and Mohamed Shariff (2012) who evaluated different species of grasses in various environments.

According to Arzani et al. (2005), DMI is a positive indicator of forage quality and ME is an important component in forming the diet of animals. However, grasses and reeds showed lower amounts of DMD, ME, DMI and RFV compared to other types of growth forms. The lower digestibility of grasses and reeds could be attributed to the different leaf forms and structure, and fibre content of forage plants (Rawnsley et al., 2002; Pontes et al., 2007; Amiri and Mohamed Shariff, 2012). Studies conducted by Arzani et al. (2006) and Ghadaki et al. (1974), Norton (1982), Ghoorchi (1995), and Amiri and Mohamed Shariff (2012) have shown that the nutritive values of grasses decrease as they mature. However, young grass shoots have a higher nutritive value than in old grass. Overall, the quality of grasses decreases with maturity (Vendramini, 2010).

3.6.4 How does mineral content in different growth forms compare to daily requirements for livestock? UNIVERSITY of the

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The daily requirements of Ca for livestock are 0.21 to 1.13% (2100-11300mg/kg) (Cunha and McDowell, 2012). Calcium concentrations of forage types for the wet and dry seasons in this study were higher than the required Ca levels (Table 3.1). Thus, the Ca concentrations in the forages in the Leliefontein communal rangeland were adequate and sufficiently high to meet the requirements of livestock. These findings were also higher than those reported by Khan et al., (2006a; 2009). These differences could be due to the difference in time of collecting forage types, the type of soil, vegetation chemical content and stage of growth.

The requirements of Mg for livestock are 0.04 to 0.25% (400-2500mg/kg) (Cunha and McDowell, 2012). Mean forage Mg concentrations of leaf succulents, trees and herbs in this study were higher than the requirements of livestock, but were also found to be higher than the findings reported by the following authors in some studies in Pakistan (Ahmad et al., 2008; Khan et al., 2009; Mirzaei, 2012), while the Mg concentrations in the grasses, non-succulent shrubs

and reeds were similar to the results reported by Khan et al., (2006b) in Pakistan. This difference in Mg concentrations might be due to differences between forage species and the level of Mg in the soil (Gizachew et al., 2002). Higher concentrations than the requirements for livestock, thus, indicate that no supplementation for livestock would be needed if they are managed properly by farmers.

Potassium concentrations in the wet and dry seasons were found to be high in most of the forage growth forms. The requirements of K for livestock are 0.5 to 1.20% (5000-12000 mg/ kg) as noted by Cunha and McDowell (2012). Potassium concentrations of forage growth forms in this study were high enough to meet the requirements of livestock This was similar to findings reported by Mirzaei (2012) in Pakistan. Khan et al. (2009) reported that there were variations in K concentrations in forages within different seasons in their study in Pakistan due to different stages of plant maturity at the time of forage sampling.

Sodium concentrations between the wet and dry seasons were not found to differ significantly (P>0.05) from each other. However, there was a variation in Na concentrations between the growth forms of forages. Sodium concentrations of reeds in the wet and dry seasons were below the requirements of livestock, 0.06 to 0.1% (600-1000mg/kg), as reported by Cunha and McDowell (2012). Furthermore, Na concentrations of trees and grasses in the wet season were below the requirements for livestock. This was in harmony with the report by Khan et al. (2007, 2009) in Pakistan. Thus, there is a possibility that livestock in Leliefontein might face some sodium deficiencies. However, the other forage plants may compensate for these low Na concentrations in these growth forms if animals consume a mixed diet.

Phosphorus concentrations in the wet and dry seasons were below the critical level of P. The P requirements of livestock is 0.16 to 0.47% (1600-4700mg/kg) (Table 1) as published in Cunha and McDowell (2012). The concentration of P of plants is influenced decidedly by the availability of P in the soil (Soetan et al., 2010). The present study showed that the P content of different plant growth forms was generally lower than the suggested level during the wet and dry seasons. These results were lower than the findings of Ganskopp and Bohnert (2003). Low P concentrations of forages in the current study could be due to P deficient soils and drought conditions (Stockdale et al., 2005). Akhtar et al. (2007) concluded that P deficient soils lead to

deficiencies in the plants grown in these soils. Hussain and Durrani (2008) in the Harboi rangeland in Pakistan observed that P contents of plants commonly decrease with the maturity of plants. On a global scale, P is probably the most frequent mineral deficiency among livestock (Ganskopp andBohnert, 2003) due to its low availability in soil to forage plants and loss through soil erosion (Hussain and Durrani, 2008).

Among the growth forms of plants in the present study, trees, non-succulents and herbs showed high CP percentages (12.12%, 7.01% and 8.36%) in the wet season. This may play an important role in meeting the animals' needs for protein as the critical level of crude protein content for ruminants is about 7% as suggested by Dasci et al. (2010). However, most growth forms of plants in the present study contained CP concentrations lower than the critical level needed by animals.



Table 3.1: The results of minerals concentrations for forage growth forms compared to daily requirements of livestock.

Growth Forms	Season	Grass	Herbs	Leaf succulents	Non- succulents	Reeds	Trees	Requirements for livestock
Ca	Wet	7534.70	10886.94	15354	9060.80	5920.18	7835.36	2100 112001
(mg/kg)	Dry	5741.41	7516.06	11913.79	8784.69	3543.73	10034.29	2100- 11300 ¹
P	Wet	0.72	1.78	1.19	1.00	0.79	1.83	1600-4700 ¹
(mg/kg)	Dry	0.60	1.30	0.98	0.70	0.29	0.87	1000-4700
Mg	Wet	1333.78	2832.13	5288.80	2561.91	949.31	3501.78	400-2500 ¹
(mg/kg)	Dry	1253.14	1830.11	5707.39	2482.77	1231.71	3051.42	400-2300
K	Wet	10702.19	15845.13	15955.87	111142.02	10532.32	15085.15	5000- 12000 ¹
(mg/kg)	Dry	5689.54	6769.36	11876.36	7514.49	5663.33	8625.54	3000- 12000
Na	Wet	829.51	1095.97	4329.78	799.02	279.80	1095.60	600-1000 ¹
(mg/kg)	Dry	368.59	735.61	2825.58	1117.10	508.01	286.37	000-1000
CP %	Wet	4.36	8.36	4.54	7.01 of the	4.90	12.12	7.5- 19 ²
C1 /6	Dry	3.51	5.60	3.24	5.18	2.39	5.35	7.5-17

1. Cunha and McDowell (2012), 2. Dasci et al. (2010)

3.7 Conclusion

The nutrient values of forages in rangeland depend on several factors which include soils and plant maturity. The nutritional values and the quality of forages differed between growth forms in the Leliefontein communal rangeland. The results showed that some forage plants with low palatability, such as leaf succulents, if combined with higher quality forage can provide the animal's daily requirements. The results also showed lower nutritional values are found in grasses and reeds than in other forage types. The forage in the Leliefontein communal rangelands is poor in quality in terms of phosphorus and crude protein content, and supplementation may be needed for grazing ruminants especially during the dry season. However, due to the diversity of forage plants in the study area, this study suggests that adequate minerals such as Ca, K, Mg and Na for livestock are available for livestock in the wet and dry seasons.

CHAPTER FOUR

Assessing Chemical Defences against Herbivory in Renosterveld Vegetation

in Leliefontein, Namaqualand

4.1 Abstract

The present study assessed the chemical defences of plants in Renosterveld vegetation in Leliefontein, Namaqualand, inferred from condensed tannin (CT), total phenolic (TP) and silica (Si) concentrations of different forage growth forms (grasses, reeds, herbs, leaf succulents, non-succulents and trees). Forage plants were collected in the dry season and wet season to investigate and compare the CT, TP and Si concentrations in the different forage growth forms; firstly, within each season and thereafter, between the two seasons. It was found that there was a high variation in the concentrations of CT and TP between different forage growth forms in the wet and the dry seasons respectively, and only non-succulents showed a significant difference in the CT and the TP concentrations between the wet and the dry seasons. Silica concentrations showed no significant differences between forage growth forms in the wet and the dry seasons, except in non-succulents and leaf succulents.

Keywords: condensed tannins, total phenolics, silica, secondary compounds.

4.2 Introduction

Secondary compounds such as polyphenols and condensed tannins are chemical defences that reduce the nutritional quality of forage plants and can influence diet selection of livestock (Scogings et al., 2011; War et al., 2012; Moles et al., 2013; Hattas, 2014). They are also known as anti-nutritional factors which are associated with plant defence mechanisms against herbivores (Schardl, 2001; Arimura et al., 2005; Van Dam, 2009; Njidda et al., 2012). Plant secondary compounds are strictly not essential for the main functions of the plants such as reproduction and growth (Forbey et al., 2009) and therefore, they are called secondary compounds. Plants can produce a large amount of secondary compounds (Epstein, 2009; Becerra, 2015) and different phenolic compounds may have different effects on herbivores (Pizarro and Bisigato, 2010).

Plants can produce a large amount of secondary compounds such as total phenolics (TP) and tannins (Epstein, 2009; Becerra, 2015). Phenolic compounds or total phenolics are secondary metabolites that play an important role in providing plants protection against herbivory by means of reduction in feed intake (Balasundram et al., 2006). Phenolics are among the most widely studied plant secondary compounds (Balasundram et al., 2006). Phenolics act as a defensive mechanism against herbivores by reducing the palatability of the plant tissues (War et al., 2012) or by means of reduction in feed intake (Balasundram et al., 2006). Condensed tannins are complex phenolic polymers which naturally occur in plants as herbivore deterrents (Li et al., 2014; Tadele, 2015) especially trees, shrubs and herbaceous leguminous plants (Frutos et al., 2004; Sadaghian et al., 2011). These compounds have both harmful and beneficial effects on mammalian herbivores.

Harmful effects of secondary metabolites in livestock have been reported when consumed forage is high in phenolics and CT concentrations (McSweeney et al., 2001; Kingston-Smith et al., 2010; Estell et al., 2014). Condensed tannins cause bitter and astringent tastes of plants (Reed, 1998; Ashok and Upadhyaya, 2012), thus, reducing the palatability of forage (Aganga and Tshwenyane, 2003; Basha et al., 2013), and consequently, lessen forage intake by livestock (Salem et al., 2005; Alonso-Díaz et al., 2008). A reduction in forage uptake has been shown to affect the growth rate and net metabolizable energy of the livestock (Štukelj et al., 2010). In

addition, consuming forages containing high level of CT (>50 g/ kg) decreases ruminal protein degradation (Min et al., 2003; Frutos et al., 2002).

The beneficial effects of phenolic compounds are dependent on the concentrations found in the plants (Puchala et al., 2005). Concentrations of condensed tannins between 5 and 55 g/kg of dry matter were found to be beneficial to ruminants, prevent bloating, increase fertility and improve overall animal well-being by limiting nematode infestations (Mueller-Harvey, 2006; Berard et al., 2011; Hattas, 2014; Min and Hart, 2003). Forages that contain CT concentrations of <5% have also been shown to have positive effects on herbivore performance (McMahon et al., 2000; Basha et al., 2012). Studies have shown that a low quantity of tannins improves utilisation of feed protein without reducing forage intake or carbohydrate digestibility (Waghorn, 1990; Wang et al., 1994; McMahon et al., 2000) and by protecting dietary proteins from redundant degradation in the rumen without affecting assimilation of fibre (Kaplan et al., 2014; Hattas and Julkunen, 2012; Osuga et al., 2006). Therefore, higher animal performance can be observed when the diet contains low amounts of CT (Schofield et al., 2001; Makkar, 2003). Furthermore, there is an increase in animal body weight, wool growth and milk production of livestock if the diet contains low amounts of CTs (Mueller-Harvey, 2006; Berard et al., 2011; Hattas, 2014).

Silica (Si) is a mineral nutrient to plants, but also plays a role as a physical defence mechanism against herbivores (Massey et al., 2007; Massey and Hartley,2009et al.,). Although Si is not one of the essential elements for plant growth (Schoelynck et al., 2010), it has an essential role in supporting plant growth in improving the structural strength of plants and in resistance against herbivores (Marafon and Endres, 2013). Silica reinforces the cell wall and precipitation of solid Si within the plant's cell wall. In addition, Si improves the structural strength of plants by forming structures such as thorns, spines, trichomes, prickles, tough epidermal cells and hard pods that vary in size and shape, and are more solid than mineral cell walls (Craine et al., 2003; Neethirajan et al., 2009; Marafon and Endres, 2013).

Silica also reduces the digestibility of grasses (Reed, 1998; Minson, 2012) by increasing the abrasiveness of the plant tissues (Massey et al., 2006; De Melo et al., 2010), which deters herbivores (Massey et al., 2007). High Si concentrations can affect the performance of herbivores (Massey and Hartley, 2006; Massey et al., 2006; Kvedaras et al., 2007) by reducing

the efficiency of food utilisation and the digestibility of food when herbivores feed on Si rich diets leading to reduced growth rates (Massey and Hartley, 2009).

Forage plants differ in their nutritional value due to differences in their nutrients and antinutritional (secondary metabolite) content (Baraza et al., 2009). Evaluating both the antinutritional components and mineral nutrient values of the forage plants allows for a better understanding of the quality of different forage plants. Consequently, this chapter explores whether there are any relationships between the nutritional value and anti-nutritional quality of TP and CT in the different forage growth forms in the Renosterveld vegetation in the Leliefontein communal rangeland in Namaqualand.

Forage plants in the Namaqualand Renosterveld vegetation of the Leliefontein communal rangeland are a food resource of livestock. Some of these resources could be of poor quality, not only because plants are low in nutrients, but also because they produce plant secondary metabolites, such as TP and CT, which may impair digestion (Dearing et al., 2005). In general, as the concentration of secondary compounds increases in the forage, intake decreases (Iason, 2005).

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4.3 Study aims and hypotheses

The aim of this study was to determine the variations of secondary compounds (TP and CT) and Si concentrations between the growth forms of forage plants within and between the wet and dry seasons. This study tested the *resource availability hypothesis* (*RAH*) that predicts that the allocation of resources to anti-herbivore defences differs between species according to their growth rate (Blumenthal, 2006). Some forage plants such as grasses are fast-growing plants and therefore, allocate most of their resources to rapid growth and as a result, may have a lower capacity to produce chemical defences (Nykänen and Koricheva, 2004). Grasses use a strategy of increased growth rate rather than investments in anti-herbivore defences to cope with herbivores (Massey et al., 2007). Slow-growing plants after growth may allocate resources to defence compounds to reduce the risk of loss by herbivores (Stock et al., 1993; Coley et al., 2006). Therefore, we predicted a high variation in TP and CT among the different growth forms.

Slow growing plants such as leaf succulents should have high concentrations of TP and CT while fast growing plants such as grasses and herbs should show low concentrations of TP and CT.

It was assumed through the *growth rate hypothesis* (*GRH*) (Coley et al., 1985) that predicts that plants found in environments rich in resources should have high growth rates and little defence Thus the concentrations of TP and CT will be higher in the dry season (summer as in the case of Leliefontein) than the wet winter season as assimilated carbon will be used for growth in the wet season.

It was assumed that grasses contain much more Si than other growth forms and that Si concentration should be higher in the wet than the dry season.

This study hypothesised that:

H1 – resource availability hypothesis

There is high variation in TP and CT among the different growth forms in that slow-growing plant should have high concentrations of TP and CT. Fast-growing plants will have low concentrations of TP and CT.

H2 –growth rate hypothesis

The concentrations of TP and CT will be higher in the dry than the wet season as assimilated carbon will be used for growth in the wet season.

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H3 - grasses contain more Si than other growth forms and Si concentrations are higher in the wet than the dry season.

To further our understanding of forage quality and the factors affecting the rate of intake by livestock in semi-arid rangelands, this study also determined whether there are any relationships between the nutritional value and anti-nutritional quality in the different forage growth forms in the Renosterveld vegetation in the Leliefontein communal rangeland in Namaqualand.

4.4 Materials and methods

4.4.1 Study site

The study was conducted in the Kamiesberg uplands of the Leliefontein communal area (30° 18′ 18′ 51′′ S, 18° 10 04′ 58′′ E) which is situated in the semi-arid Namaqualand region of South Africa.

4.4.2. Sample collection

The sample collection procedure is comprehensively discussed in Chapter Three since the same plant samples were evaluated for nutritional and anti-nutritional content.

4.4.3 Chemical analysis (TP and CT)

Total phenolics and CT were analysed using the protocol suggested by Hagerman (2002). Total phenolics were quantified using the Prussian blue assay for total phenolics (Price and Butler, 1977) and the Acid Butanol method as modified by Hagerman (2002) was used to assess CTs (Hattas et al., 2005). *Sorghum* tannin that was previously extracted and purified as described in Hattas and Julkunen-Tiitto (2012) was used as a standard for CT. To standardise TP, Gallic acid was used (Hagerman, 2002).

4.4.4 Silica

The sulphuric-peroxide digestion method (Moore and Chapman, 1986) was used to digest plant material. A 0.4 g sample of the dry, milled plant material was digested in 5 ml of sulphuric-peroxide digestion mixture in a heating block, as described by Moore and Chapman (1986). After digestion, the samples were allowed to cool to room temperature after which they were filtered through Whatman No 1 filter paper into a 100 ml volumetric flask and diluted to volume with distilled water (dH₂O).. After dilution, the samples were stored for further analyses. The digested samples were later analysed for Si. Silica concentrations were determined using Inductively Coupled Plasma Atomic Emission Spectrophotometry (ICP-AES).

4.5 Statistical analysis

To test the data for normality the Shapiro-Willks test was used. Due to the data not being normally distributed, Kruskal-Wallis analysis was performed to determine whether there were statistical significances (P <0.05) in CT, TP and Si concentrations between the different forage growth forms in the wet and dry seasons. A *t*-test was used to determine whether growth forms between the wet and dry seasons were significantly different.

To examine if there were any relationships between CP, NDF and ADF, and TP and CT the nonparametric Spearman's correlation for the different forage growth forms in the wet and dry seasons were performed The Statistical Package for the Social Sciences 23 (SPSS Inc., Chicago IL) was used for data analysis.

A principal component analysis (PCA) was used to examine forage quality of the species based on the information provided from the results. The Categorical Principal Component Analysis was used to investigate multivariate relationships among our variables and to explore the relationships among all traits simultaneously. This analysis allows the existence of a non-linear relationship between nutritional and anti-nutritional values of different forage growth forms in two seasons.

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4.6 Results

4.6.1 Total phenolic, Condensed Tannins and Silica concentration in the wet and dry season

The results of this study showed high variation in the total phenolics and condensed tannin concentrations of different forage growth forms in the wet and dry seasons (Figure 4.1, 4.2). The results further revealed that silica concentrations were not significantly different among the forage growth forms in the wet and dry seasons (Figure 4.3).

4.6.1.1 Total phenolic (TP)

There were significant differences in TP concentrations in the wet season ($H_{(6,111)} = 31.546$, p<0.001, Figure 4.1**A**), and the dry season ($H_{(5,87)} = 34.526$, p<0.001, Figure 4.1**B**). In the wet season, TP in leaf succulents was significantly higher than grasses and herbs (nine and two fold, respectively), whereas TP in trees was significantly higher (10 fold) than in grasses (p<0.05). No significant differences were found between grasses, herbs and reeds (p>0.05, Figure 4.1**A**). In the dry season, TP in leaf succulents was significantly higher than grasses and herbs (10 and four fold, respectively), whereas TP in trees was significantly higher (eight fold) than in grasses (p<0.05). However, in the dry season, no significant differences were observed between grasses, herbs and reeds, and also not between leaf succulents, trees and reeds (Figure 4.1**B**).

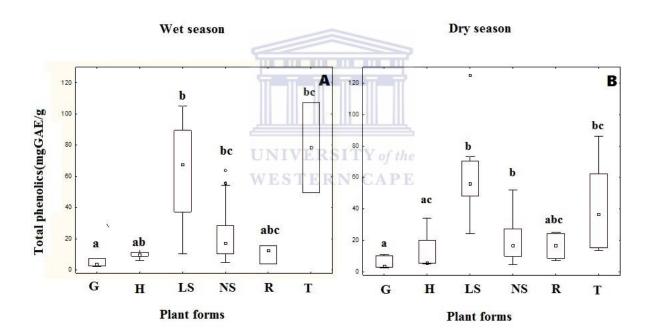


Figure 4.1: Total phenolics (TP) concentrations of different forage growth forms in dry and wet seasons. The letters A and B indicate to the number of figures. Different letters above the bars indicate significant differences between different forage growth forms in each season. G: grasses; H: herbs; LS: leaf succulents; NS: non-succulents; R: reeds; and T: trees.

4.6.1.2 Condensed Tannins (CT)

There were significant differences in CT concentrations in the wet season (H_(6,111) =25.045, p<0.001, Figure 4.2A) and the dry season (H_(5,87) =28.624, p<0.001, Figure 4.2B). In the wet season, CT in leaf succulents was significantly higher than grasses, herbs and non-succulents (34, 119 and nine fold, respectively) (Figure 4.2A). In the dry season, CT in leaf succulents was also significantly higher than grasses, herbs and non-succulents (139, 279 and 16 fold, respectively). Significant differences were also obtained between trees, grasses and herbs. There were no significant differences between grasses, herbs, reeds and non-succulents in the dry season (Figure 4.2B).

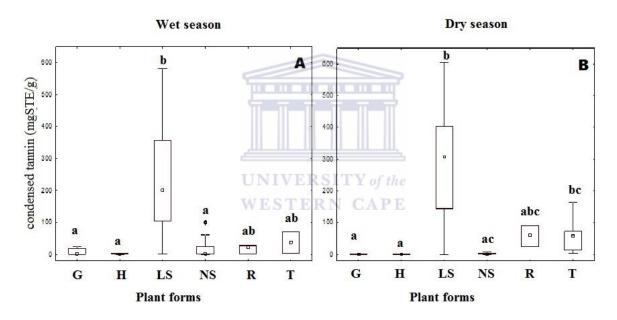


Figure 4.2: Condensed tannin (CT) concentrations of different forage growth forms in dry and wet seasons. The letters A and B indicate to the number of figures. Different letters above the bars indicate significant differences between different forage growth forms in each season. G: grasses; H: herbs; LS: leaf succulents; NS: non-succulents; R: reeds; and T: trees.

4.6.1.3 Silica (Si)

There were no significant differences in Si concentrations in the wet season between all growth forms in the both wet season ($H_{(6,111)} = 12.926$, $p \ge 0.05$, Figure 4.3**A**) and the dry season ($H_{(5,87)} = 7.178$, $p \ge 0.05$, Figure 4.3**B**)

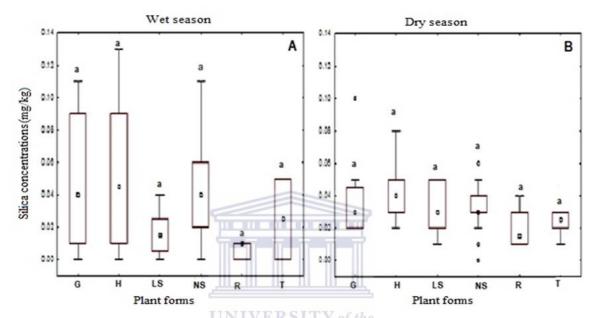


Figure 4.3: Silica concentrations of different forage growth forms in the wet and the dry season. The letters A and B indicate to the number of figures. Different letters above the bars indicate significant differences between different forage growth forms in each season. G: grasses; H: herbs; LS: leaf succulents; NS: non-succulents; R: reeds; and T: trees.

The Principal Component Analysis (PCA) showed 84.48 % of the variation in secondary compounds is explained by the first two factors (Figure 4.4). According to the PCA, leaf succulents are low in forage quality due to the high concentrations of CT and TP. However, leaf succulents showed high variation between samples. Grasses and herbs are very low in defence compound concentrations. Non-succulents are intermediate in terms of chemical defence concentrations.

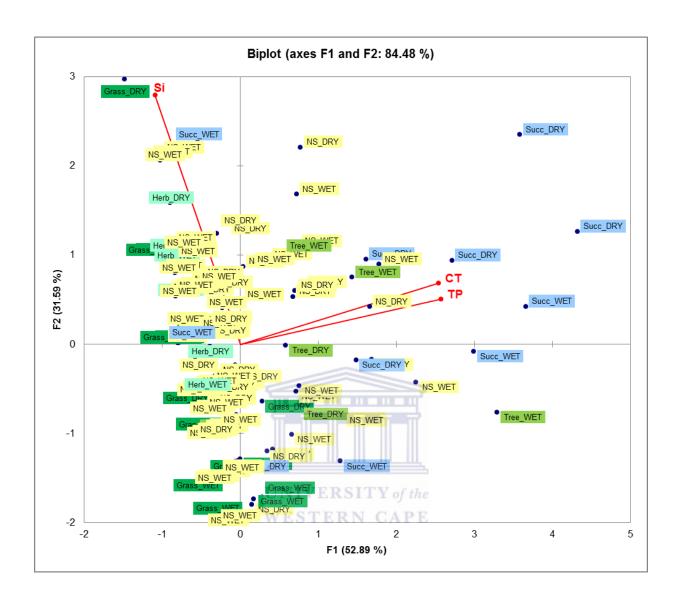


Figure 4.4: The Principal Component analysis biplot of secondary compounds (F1) and plant growth forms (F2).

4.6.2 Effect of season on expression of TP, CT and Si within different growth forms

4.6.2.1 Total phenolic

There were no significant differences in TP concentrations between the two seasons for all different forage growth forms (p>0.05, Table 4.1).

4.6.2.2 Condensed tannin (CT)

The CT concentrations in each forage growth forms were not significantly different (p>0.05) between the two seasons, with the exception of non-succulents, which were significantly different (t= 2.687, p<0.05) between the two seasons. In the wet season the CT concentrations in non-succulents were significantly higher than in the dry season (Table 4.1).

4.6.2.3 Si concentration

The results of Si concentrations showed no significant differences between the two seasons for grasses, herbs, reeds and trees (p>0.05). However, Si in NS and LS were significantly different (t=2.794, p<0.01 and t=2.412, p=0.029, respectively) between the two seasons, whereas Si concentrations in non-succulents were 1.6 fold higher in the wet season than the dry season. However, Si in leaf succulents was twofold higher in the dry season than in the wet season (Table 4.1).

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Table 4.1: Total phenolics (TP), condensed tannin concentrations (CT) and Silica (Si) concentrations of different growth forms (mean \pm SE) between the two seasons G: grasses; H: herbs; LS: leaf succulents; NS: non-succulents; R: reeds; and T: trees. Different letters (a and b) indicate significant differences between the two seasons for each forage growth form.

Grow	vth forms	Wet season	Dry season	P-value
	G	6.68 ± 2.69^{a}	5.9 ± 1.34^{a}	0.912
	Н	26.10 ± 16.40^{a}	14.03 ± 5.75^{a}	0.44
TP	LS	63.00 ± 11.50^{a}	62.49 ± 9.20^{a}	0.677
(mg/g)	NS	22.04 ± 1.97^{a}	21.3 ± 1.95^{a}	0.987
(1118/8)	R	10.50 ± 3.40^{a}	16.5 ± 4.6^{a}	0.374
	Т	78.41 ± 28.65^{a}	41.67 ± 11.60^{a}	0.194
	G	7.02 ± 3.99^{a}	2.13 ± 1.34^{a}	0.267
	н 🦷	2.75 ± 1.46^{a}	0.90 ± 0.55^{a}	0.139
	LS	$238.95 \pm 67.86^{\mathbf{a}}$	$279.52 \pm 67.00^{\mathbf{a}}$	0.677
CT	NS	24.23 ± 5.06^{a}	$17.8 \pm 5.25^{\mathbf{b}}$	0.02
(mg/g)	R	16.61 ± 8.12 ^a	61.7 ± 13.90^{a}	0.052
	T	37.64 ± 34.45^{a}	$61.99 \pm 23.40^{\mathbf{a}}$	0.613
	G	0.046±0.016 ^a	0.039±0.009 ^a	0.708
	Н	0.054±0.015 ^a	0.044±0.01 ^a	0.604
Si (mg/kg)	LS	0.016±0.004 ^a	0.033±0.005 ^b	0.029
(mg/ng)	NS	0.052 ± 0.008^{a}	0.032±0.001 ^b	0.004
	R	0.007±0.003 ^a	0.02±0.007 ^a	0.141
	Т	0.025 ± 0.025^{a}	0.023±0.003 ^a	0.904

4.6.3 Relationships between chemical defenses (TP andCT), crude protein and fiber (NDFandADF) in different forage growth forms

There was a strong negative correlation of CP with NDF in grasses and herbs in the wet season, whereas no correlation was found in the dry season (Table 4.2). CP showed a strong negative

correlation with ADF in herbs in the wet season and in grasses in the dry season. However, CP showed a weak correlation with ADF in non-succulents in the wet season and the correlation was positively weak in the dry season for non-succulents (Table 4.2). We observed a weak negative correlation between CP and TP contents in non-succulents in the wet season. TP showed a strong negative relationship with NDF and ADF in reeds in the dry season. A strong negative relationship was also found between TP and ADF in herbs and with NDF in grasses in the wet season, but was weak in non-succulents in the dry season. A strong negative correlation of CT was found with NDF and ADF in leaf succulents in the dry and wet seasons. A significant negative correlation was also evident between TP and CT, and NDF in grasses (Table 4.2).



Table 4.2: Spearman's correlation coefficients between TP and CT, crude protein, NDF and ADF in different forage growth forms in the wet and dry seasons.

Growth Forms	Wet season					Dry season			
		TP	CT	NDF	ADF	TP	CT	NDF	ADF
Grasses	CP	0.464 ^{NS}	0.321 ^{NS}	-0.786*	-0.643 ^{NS}	0.452 ^{NS}	0.119 ^{NS}	-0.619 ^{NS}	-0.762*
	TP		0.964**	-0.821*	-0.714 ^{NS}		0.429 ^{NS}	-0.667 ^{NS}	-0.190 ^{NS}
	CT			-0.786*	-0.643 ^{NS}			$0.048^{\rm NS}$	-0.024 ^{NS}
	NDF				0.857^{*}				0.667 ^{NS}
Herbs	CP	0.285 ^{NS}	-0.115 ^{NS}	-0.915**	-0.733*	0.600 ^{NS}	0.700 ^{NS}	-0.700 ^{NS}	-0.700 ^{NS}
	TP		-0.176 ^{NS}	-0.115 ^{NS}	-0.152 ^{NS}		0.500 ^{NS}	-0.900*	-0.900*
	CT			0.285 ^{NS}	$0.042^{\rm NS}$			-0.800 ^{NS}	-0.800 ^{NS}
	NDF				0.855**				0.950**
Leaf succulents	~~	0.000	0.110	0.540	0.5100	T		T	
	CP	-0.238 ^{NS}	0.119 ^{NS}	-0.619 ^{NS}	-0.619 ^{NS}	0.050 ^{NS}	-0.083 ^{NS}	0.317 ^{NS}	0.333 ^{NS}
	TP		0.738*	-0.524 ^{NS}	-0.524 ^{NS}		0.617 ^{NS}	-0.417 ^{NS}	-0.350 ^{NS}
	CT			-0.833*	-0.833*			-0.883**	-0.900**
	NDF		للللم		0.984**				0.983**
		·	TINIT	VEDELT	W collection	I			
Non-	CP	-0.293**	-0.173 ^{NS}	-0.189 ^{NS}	-0.265*	-0.259 ^{NS}	-0.164 ^{NS}	-0.275*	0.287*
succulents	TP		0.650**	0.312**	-0.271*		0.562**	-0.388**	0.352**
	CT			-0.080 ^{NS}	-0.039 ^{NS}			-0.169 ^{NS}	-0.122 ^{NS}
	NDF				0.945**				0.988**
Reeds	CP	-0.500 ^{NS}	-0.988**	-0.500 ^{NS}	0.557 ^{NS}	0.800 ^{NS}	$0.800^{ m NS}$	-0.400 ^{NS}	-0.800 ^{NS}
	TP		0.500^{NS}	0.987**	0.116^{NS}		1.000**	-0.800 ^{NS}	-0.833**
	CT			0.500^{NS}	-0.500 ^{NS}			-0.800 ^{NS}	-0.888**
	NDF				$0.850^{ m NS}$				0.800^{NS}
Trees		1				1		T	,
	CP					-0.486 ^{NS}	-0.429 ^{NS}	-0.143 ^{NS}	-0.143 ^{NS}
	TP						0.771^{NS}	-0.371 ^{NS}	-0.371 ^{NS}
	CT							-0.257 ^{NS}	-0.257 ^{NS}
	NDF								0.985**

^{**} P< 0.01, *P< 0.05, note: replication in tree samples were inadequate (only 2) in the wet season.

4.6.4 Relationships between all the variables measured during the study

The first axis explained 47.07% of the variation. The second axes explained 13.28% of the variation. It shows that grasses are more associated with higher fibre contents whereas leaf succulents have high secondary compound concentrations. Non-succulent shrubs have the highest relative forage values during the wet season (Figure 4.5).

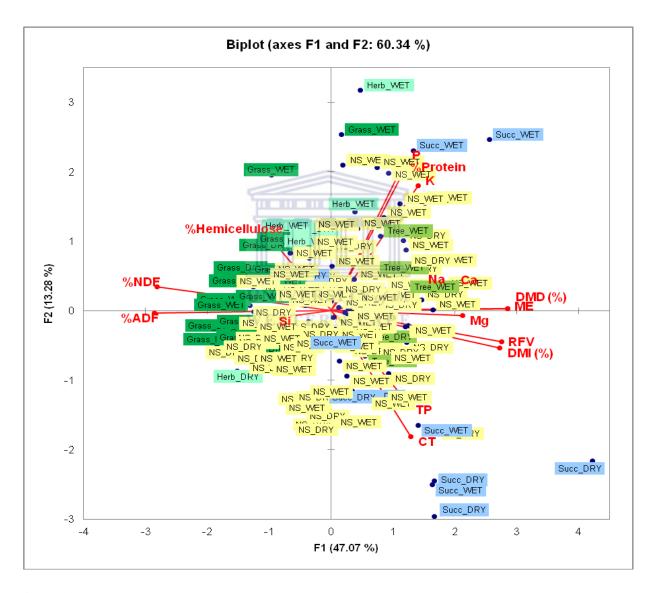


Figure 4.5: The principal component analysis biplot of the variables measured during the study (F1) and plant growth forms (F2).

4.7 Discussion

Plant secondary compounds greatly influence food selection and nutritional value of plants because they reduce digestibility (Palo et al., 2012). More information on forage quality is provided by measuring TP and CT concentrations in forage plants rather than CT alone (Waghorn, 2008).

Hypothesis 1

Hypothesis 1 could be accepted since the present study showed that TP and CT concentrations showed high variations among the different forage growth forms in the two seasons. Slow-growing leaf succulents and trees had significantly more TP and CT than faster growing grasses, reeds and herbs. Non-succulent TP and CT concentrations were mixed because the growth form include both slow and fast growing plants.

Some forage plants such as grasses and herbs are fast-growing and therefore, allocate most of their resources to rapid growth and as a result, may have a lower capacity to produce chemical defences (Nykänen and Koricheva, 2004). Grasses generally use a strategy of increased growth rate, rather than investments in anti-herbivore defences to cope with herbivory (Massey et al., 2007). Herbivores thus prefer to consume fast-growing species (Blumenthal, 2006). Samuels et al., (2015) who used direct observations of livestock grazing in the field of the current study area found that livestock prefer to consume grasses and herbs rather than other forage growth forms, which might be due to low secondary compound concentrations in these forage species as this study also indicates. However, herbivores need to consume a diversity of plant species that contain different kinds of compounds. Thus, Samuels et al., (2015) observed that livestock (goats and sheep) fed on non-succulent shrubs in the dry season.

Slow-growing plants such as leaf succulents and trees after growth may allocate resources to defence compounds to reduce the risk of loss by herbivores (Stock et al., 1993; Coley et al., 2006). Thus, because the inherent growth rate determines the opportunity of defence produced (Endara and Coley, 2011), this could be one of the major reasons for the significant variation between different forage growth forms in chemical defence in the current study.

However, the observed concentrations of CT in grasses, herbs, non-succulents and reeds were lower than the tolerable limit of 5.5% of dry matter in the wet and the dry season. Thus it could generally be considered unlikely to have a significant effect on digestion of nutrients by the ruminants (Frutos et al., 2002; Basha et al., 2012). In the leaf succulents however the levels of TP and CT concentrations were excessively high relative to other growth forms. These extremely high concentrations may suppress feed intake and growth of the livestock due to decreased palatability of forage. Condensed tannins may also decrease digestive efficiency and animal productivity (Makkar, 2003; Berard et al., 2011). This might be the reason why leaf succulents were rarely consumed by livestock in the Leliefontein communal area (Samuels et al., 2015). This high anti-nutritional content found in leaf succulents have most likely evolved as a defence mechanism against herbivores (Pizarro and Bisigato, 2010). In addition, reduced consumption and avoidance of bitter compounds of forage is also a behavioural strategy herbivores use to cope with CTs (Estell, 2010).

Herbivores consume a variety of plant species in rangelands, even those that contain different forms and quantities of secondary compounds in order for them to meet their nutritional needs (Lyman et al., 2008). Therefore, livestock could select forages with a higher ratio of protein to energy after they consume forages that contain high concentrations of CT which is widespread in the plants (Baraza et al., 2005). Furthermore, livestock have the ability to detoxify or tolerate consumed toxins. Therefore, livestock could better meet their requirements for nutrients and regulate their intake of toxins (Papachristou et al., 2005).

Hypothesis 2

Hypothesis 2 could not be accepted for all the growth forms with the exception of non-succulent shrubs. This is because the concentrations of TP and CT in grasses, herbs, leaf succulents, trees and reeds were similar between seasons for each of the growths. However, non-succulents showed a significant difference in CT concentrations between the two seasons. The significant difference might be because of the plants' growing conditions from season to season (Li et al., 2014). Seasonal variation in rainfall and resources is also linked with the phenological stage due to the different demands for nutrients by plants (Milla et al., 2004).

In the wet season with an abundance of rainfall, forage plants generally have high nutrient concentrations and low secondary metabolite concentrations (Scogings et al., 2015). However, in the dry season there is a reduction in rainfall and this could significantly affect the TP and CT concentrations in plants and the responses of secondary metabolites to resource availability could cause the significant difference of the non-succulents (Scogings et al., 2015). Furthermore, the difference of CT concentrations in non-succulents between seasons could be explained by the growth-differentiation balance hypothesis, which proposes that there is a physiological trade-off between growth and secondary compounds in plants and predicts effect of resource availability such as water or nutrients on production of secondary metabolites such as CT (Pizarro and Bisigato, 2010). This study thus supports these two hypotheses that predict increased carbon allocations to secondary compounds under low nutrient conditions, but for non-succulents only (Ferwerda et al., 2006; Zhang et al., 2009).

During their growth period, plants produce a lot of biomass; thus, few resources are available for the synthesis of phenolic compounds. However, during flowering, excess carbon might be obtainable for condensed tannin production (Frutos et al., 2004). Furthermore, Salem et al., (2006) and Njidda et al., (2012) also found high amounts of phenolics and condensed tannins in browsed tree foliage native to the semi-arid region of northern Egypt in the dry season and in the semi-arid regions of northern Nigeria respectively. However, comparisons are very complicated with other published CT concentration studies for similar growth forms due to variations in methods, procedures and standards used for the analysis.

Hypothesis 3

Grasses have the ability to take up large amounts of Si from the soil where it contributes to their mechanical strength (Heckman, 2013). Therefore, grasses should contain high concentrations of Si, about 1.5% (15 g/kg) (Smis et al., 2014).

In the present study, Si concentrations in grasses did not support our hypotheses that grasses contain high silica. The highest amount of Si in the present study was less than 0.1 mg/kg measured in herbs. Significant differences in the Si concentrations between the wet and the dry seasons were observed in non-succulents which were higher in the wet than the dry seasons and

leaf succulents, where the Si concentrations were higher in the dry season than the wet season. However, there was no seasonal effect on the other forage growth forms. The significant differences in the Si concentrations observed in non-succulents and leaf succulents between the wet and the dry seasons could be due to variations in precipitation which cause differences in the soluble Si concentrations of the soil in which they are grown. Accumulation of Si also differs greatly between plant species because of differences in the plants Si uptake ability (Ma and Yamaji, 2006). Silica concentrations differ with the growth stages of plants; older plants contain higher Si concentration in their tissues. Some species of grasses contain low concentrations of silica: that was unpredicted in the study (Labun et al., 2013).

The beneficial effect of Si is that Si protects plants from multiple abiotic and biotic stresses (Ma and Yamaji, 2006). However, numerous plants are not able to accumulate high concentrations of Si to be beneficial.

In this study, very low concentrations of Si were observed for all forages, which might be due to low Si availability in the soil (Heckman, 2013). However, soil concentrations were not evaluated in this study. Indications of low Si are not usually observed in the field (Heckman, 2013).

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4.7.1 Relationships between TP and CT, and crude protein, NDF and ADF

The negative correlation between CP and ADF in herbs indicates that the quality of herbs decreases with a decrease in CP (Teka et al., 2012). The results of this study also showed a negative correlation between CP and CT contents in reeds, which contrasts with a previous study done by Zhang et al., (2009), but is consistent with a study conducted by Kraus et al. (2004). The negative correlation between chemical defences and fibre might be due to the fact that, for example, grasses contain high fibre concentrations and low CT concentrations. This is similar to the findings of Zhang et al. (2009) who also found a negative correlation between CP and TP which supported the hypotheses that predicted increased C allocation to secondary C compounds under low nutrient conditions (Zhang et al., 2009). Therefore, it is common to find a negative correlation between CP and secondary compound contents such as phenolics and tannin (Mansfield et al., 1999).

4.8 Conclusion

In this study, non-succulents have good quality in terms of low concentrations of CT. The different TP and CT concentrations of different forage growth forms can thus affect the quality of forage and forage intake. From the results of the forage plants, it was found out that the leaf succulents had the highest concentrations of CT indicating that they may have low forage quality and low palatability. However, grasses and herbs showed good quality for livestock in terms of a low amount of secondary compounds. The results revealed that grasses and non-succulents are similar in terms of the concentration of anti-nutritional compounds

The low concentrations of Si found for all forages, might be due to low Si availability in the soil. However, a limitation of this study was that we did not test the soil for Si and further studies need to analyse Si in soil. By studying the correlations between the different variables of different forages in the current study, it gives us an indication of the extent of the differences in the nutritive values and secondary compounds that affect the quality of forage. Animal selection could favour different levels of defences in plant species with different inherent growth rates.

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CHAPTER FIVE

GENERAL CONCLUSION

5.1 Introduction

The study was conducted in Namaqualand Renosterveld vegetation in the Leliefontein communal area, where the predominant land uses in this area is extensive livestock grazing. Namaqualand is part of the Succulent Karoo Biome (Todd and Hoffman, 1999) which is semi-arid and has a Mediterranean type climate. Knowledge of the nutritional quality of the forage plants available to grazing animals will help identify potential mineral nutrient deficiencies, and also aid in the development of strategies to supplement the required elements (Arzani et al., 2006).

Moreover, the information obtained on the quality of the available forages could help rangeland managers to strike a balance between animal requirements and available forages to reach maximum animal performance (Arzani et al., 2011). The nutritive values of different plant growth forms (grasses, reeds, herbs, leaf succulents, non-succulents and trees) were evaluated by analysing the quantities of mineral nutrients, crude protein, fibre and energy of plant materials as these are good indicators of forage quality (see Chapters 3 and 4; Arzani et al., 2006). Livestock production is related to the amount of nutrients in the forage. Hence, determining the nutritional value of forages is important for livestock production and the subsequent management of livestock (Schut et al., 2010). However, doing chemical analysis for the nutritional value of plants needs to go hand in hand with determining the anti-nutritional quality such as the secondary compound composition of the plants as this will lead to a better understanding of the overall quality of the available forage plants.

5.2 Study conclusions

Complex interactions exist between the nutritional and anti-nutritional values of different forage plants as indicated by the literature. Very little information exists regarding the quality of

available forage plants to livestock in the wet and dry seasons in the Namaqualand Granite Renosterveld vegetation type. The aims of the current study were, therefore, to determine the mineral nutrient, crude protein and fibre (ADF and NDF) content, as well as the anti-nutritional quality in terms of condensed tannin, total phenolics and silicon concentrations of the different forages available to the livestock in the wet and dry seasons in the Leliefontein Communal Rangeland.

Forages have a combination of physical, chemical, and structural characteristics that determine the quality of forage in rangelands and indicate the nutritive value of it to animals (Corson et al., 1999). We concluded that forage quality varies greatly among the different forage growth forms within each season. Results of this study revealed that non-succulent plants are better quality compared to other types due to the amount of high nutrition concentrations which can meet the needs of livestock in the study area, and they also contain low levels of anti-nutritional compounds. However, trees and herbs have good forage quality due to high crude protein concentration and minerals. Grasses could also be considered good forage due to their low levels of secondary compounds.

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5.3 Answering the overall study questions **EXAMPLE**

The objective of this chapter was to answer the following research questions set out in the introduction by using the knowledge gained through this study:

- **1.** Are there variations in nutritional values between different forage growth forms within and between the dry and wet seasons?
- **2.** Are there variations in secondary compounds between different forage growth forms within and between the dry and wet seasons?
- **3.** Is there a relationship between plant chemical defences and forage nutrition in Renosterveld vegetation?

5.3.1 Are there variations in nutritional values between different forage growth forms within and between two seasons?

The present study showed that mineral nutrient concentrations, fibre, crude protein content and digestibility varied between the different forage growth forms in the dry and wet seasons. Chapter Three showed that the nutritional quality of the different forage growth forms showed significant differences within each sampling season. Some forage plants, especially leaf succulents, had high digestibility and contained large amounts of mineral nutrients in both the wet and dry sampling periods. The mineral concentrations in relation to livestock requirements were generally adequate to satisfy the requirements of the livestock in both seasons.

However, in certain forage types, Na and P concentrations were below the critical levels. Phosphorous concentrations were deficient in all forage growth forms in this study as none of the forages met the daily requirements of phosphorus by livestock in the two seasons. There were no significant differences between the two seasons within each forage type in most minerals. In this study, we also confirmed that the CP content of most growth forms is very low in the dry season. Leaf succulent plants in this study area showed the highest mineral nutrient concentrations, DMD and ME. Leaf succulents were also low in fibre, which indicates good quality and desirable forage.

5.3.2 Are there variations in secondary compounds between different forage growth forms within and between two seasons?

In this study, secondary compounds, TP and CT concentrations of forages varied to a great extent between forage growth forms within the two seasons. We also found that leaf succulents in the study area contained the highest level of chemical defences which is considered as an indicator of lower quality of the forage. Silica concentrations of all growth forms were very low in the wet and dry seasons.

5.3.3 Is there a relationship between chemical defences and forage nutrition?

The results of this study indicate that there are significant relationships between nutrition and anti-nutrition compounds in forage plants. Thus, the quality of forage plants in rangelands is reflected by both the concentration of nutrients and secondary compounds in available forage plants. This suggests that both of these quality parameters are essential in order to draw meaningful conclusions regarding forage quality of these rangeland plants. Forage quality information will help the rangeland managers to determine grazing capacity, balance the animal requirements with available forage and achieve optimum livestock performance in the study area. Understanding forage quality and the factors that affect its constituents will help improve livestock production by making decisions that optimise forage nutritive value and intake.

It can also be concluded that knowledge of the relationship between nutritive and anti-nutritive factors which affects the quality of forage could give us a better understanding of how livestock select vegetation for consumption and will further allow us to develop an appropriate grazing management of rangelands.

5.4 Recommendations and future studies

There is variation in forage quality among species within each growth form. Further research is needed at species level in order to determine which plant species are the most nutritious in terms of both nutritional quality and anti-nutritional quality. It is recommended that the plant species and the stage of maturity of the forage plants should be covered in future studies to gain a better understanding of the correlation between plant quality and anti-quality factors over the life cycle of the plants.

This study only tested NDF and ADF to determine fibre, but did not investigate the content of lignin and it is thus suggested that further research be conducted on this as a forage quality indicator. Another contributing factor to forage quality is soil composition and soil analysis is proposed for future studies. This will give more information about the variation in mineral nutrients and Si content of different growth forms during different seasons. Finally, the most important study to be conducted within this study area is the correlation between chemical composition of forages and animals' preference for a specific plant.

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