SPATIAL-TEMPORAL VARIATION IN FORAGE RESOURCE PRODUCTION IN RICHTERSVELD NATIONAL PARK, SOUTH AFRICA

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DECLARATION

This thesis is my original work and has not been presented for a degree in any other University or for any other award

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I dedicate this work to my family namely Peter Mwangi, Bridget Wairimu and Hope Njeri.

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ABBREVIATIONS AND ACRONYMS

NRP	Richtersveld National park
FPAR	Fraction of Photosynthetic Active radiation
MODIS	Moderate Resolution Imaging Spectroradiometer
GLM	General Linear Model
ANOVA	Analysis of Variance
CCA	Canonical Correspondence Analysis
DWAF	Department of Water and Forestry
ANPP	Above-ground Net Primary Production
NDVI	Normalized Difference Vegetation Index

ABSTRACT

Forage production and distribution in rangelands is not uniform but varies with seasons and between landscapes. In arid ecosystems such as Richtersveld National Park (RNP), biotic and abiotic factors affects forage production. Therefore, there is need to understand how these factors affect forage production in RNP, and how forage production vary in space and time. The aim of the study was to assess the effects of biotic and abiotic factors on plant biomass production, species composition and diversity of annual-dominated vegetation in RNP; to assess the spatial and temporal variation in forage production by shrubs and factors that influence forage production and variability in RNP; and to quantify spatial and temporal variation in browse production by seven tree species along the riparian zone and determine the factors that influence browse production in RNP. Stratified sampling of vegetation and soil was done in the five vegetation types found in RNP. Mobile exclosures were placed at 100 m, 500 m and 1000 m from the stock posts to exclude grazing. Soil samples were collected at the same sample plots. Harvest method of clipping vegetation of the current year's growth was used to calibrate Fraction of Photosynthetic Active Radiation (fPAR) values from remotely sensed MODIS imageries. To determine variation in browse production by trees, plants of the seven most abundant tree species were sampled in three study sites along the river. Biomass production and species diversity of annual plants differed significantly ($P<0.05$) with distances from the stock posts. Biomass production, species richness and diversity of annual plants were positively correlated to rainfall and soil nutrients. Biomass production by shrubs was significantly higher ($P<0.05$) in Succulent Karoo than in Desert biome. There was a strong relationship between biomass production and fpar values. *Ziziphus mucronata (*Willd.), *Rhus pendulina (*Dr.J.P. Roux) and *Acacia karoo (*Hayne) were found to be the most browsed tree species by goats. Browse production differed significantly ($P<0.05$) between the tree species but did not differ between the study sites. Leaves and twigs contributed the highest components of litter. Knowledge spatial-temporal variation in forage production is beneficial in the development of adaptive management policies that would support pastoralism and conservation of plant species in arid ecosystems worldwide. An Integrated Ecological Modelling of biotic, abiotic and social economic factors is recommended for clear understanding of various dynamics found in arid ecosystems. Further studies on the nutritive value of browse forage found in RNP are recommended as well as mapping and identification of landscapes with threatened plant species in RNP.

CHAPTER 1: INTRODUCTION

1.1 Background

Rangelands are generally regarded as ecosystems where forage availability is controlled by herbivore density with a pattern of negative feedback which eventually produces a long-term equilibrium between plants and herbivores (Deng *et al.*, 2013). It has however been argued that in arid and semi-arid rangelands highly variable abiotic factors especially precipitation, have a greater influence on primary productivity and plant species composition than grazing (Tefera, 2013). This is due to the fact that plant growth in arid ecosystems depends on rainfall which regulates the diversity and abundance of plants (Anderson and Hoffman, 2011, Palmer *et al.*, 2015).

Different studies have shown that both grazing and precipitation affects vegetation composition, richness, cover and production in arid ecosystems. In ecosystems where equilibrium dynamics predominate, grazing at high animal densities impact on vegetation as vegetation growth is directly influenced by animal density (Hempson *et al.*, 2015). Other major impacts of heavy grazing that have been observed in arid rangelands are shifts in plant composition evidenced by replacement of perennial shrubs with annual plants and palatable perennial species with unpalatable ones respectively (Deng *et al.*, 2013). Anderson *et al.*, (2010) found replacement of perennial plants by annual plants in grazed areas in Mongolian arid rangelands, while Schmiedel *et al.*, (2016) observed the same trend in the Succulent Karoo, South Africa. Studies in Namaqualand have reported species composition change (Anderson *et al.,* 2010) and decreases in species diversity and cover with increasing grazing intensity (Hendricks *et al.,* 2005b; Rutherfold and Powrie, 2010). Changes in species composition and distribution due to heavy grazing result in a loss of species heterogeneity as vegetation becomes increasingly homogenous in composition (Jeddi and Chaieb, 2010).

Variability in variable abiotic factors such as rainfall have been found to influence forage availability in arid and semi-arid areas which are characterized by short growing seasons, high frequencies of drought and great intra and inter-annual rainfall variability, which result in fluctuations of primary production from year to year (Sassi *et al.,* 2009; Jeddi and Chaieb, 2010). This is particularly true for annual-dominated vegetation because the biomass of annual plants is especially strongly rainfall-driven (Anderson *et al.,* 2010). Therefore, rainfall has a greater influence on vegetation growth than grazing thus resulting in a disequilibrium dynamic whereby biomass production is uncoupled with herbivores density. In disequilibrium dynamics, Anderson *et al.,* (2010) reported that while grazing has a pronounced effect on species composition (which may only become significant over a long period), rainfall variability has an overriding effect on biomass production from year to year.

Richtersveld National Park is characterized by a distinct wet season resource that herbivores utilize during the rainy seasons and a dry key resource area along Orange River during the dry period. Key resource areas are the grazing reserve or fallback areas that herbivores utilize during the dry periods (Samuels *et al*., 2013). They help to improve the survival of herbivores, improve the body conditions and productivity of herds and also reduce the negative impact on rangelands (Samuels *et al*., 2019).

Use of key resource areas during dry seasons was found to increase the mismatch between herbivores population size and forage availability (Hempson *et al*., 2015). Greater temporal variation of the forage is likely to reduce the mean population sizes of herbivores because populations would decline during low rainfall years and rapidly recover during high rainfall years (Hendricks *et al.,* 2005b).

Herd mobility to different landscapes between wet and dry seasons in RNP, has been used as a response to temporal and spatial heterogeneity in this arid ecosystem. So management policies in arid ecosystems such as RNP should embrace the complexity of spatial and temporal heterogeneity to enable adaptive management of pastoralism as this will reduce negative effects of climatic variability on pastoralism and rangeland conditions (Samuels *et al.,* 2019).

Presence of a large key resource such as the Orange River riparian zone in RNP which animals relies on when there is no rainfall and forage is likely to influence the equilibrium between availability of vegetation and herbivore populations in a rangeland. According to Hempson *et al.*, (2015), alternating wet and dry seasons allows a grace period for plants to grow and this eventually results to forage abundance and supply needed to sustain herbivores populations in arid ecosystems. During the dry season when there is low vegetation growth, animals migrate to the key resource area along the river and this has enabled pastoralists in RNP to sustain their herds' populations throughout the years. Partitioning of grazing areas during the wet and dry seasons is beneficial in sustaining the herbivore populations and in reduction of their negative effects on vegetation growth.

In arid rangelands animal populations are regulated by forage availability in a density-dependent manner in an equilibrium dynamics (Vetter, 2005). Due to low forage supply during the dry season, animals lose weight, their reproduction rate reduce and if drought persists for a long period of time they eventually die due to lack of water and forage thus reducing their population size (Hendricks *et al.*, 2005b; Hempson *et al.*, 2015). In such a scenario the herbivore populations are at equilibrium with forage supply (Hempson *et al.*, 2015)). This equilibrium relationship between numbers of herbivores and forage supply may be countered by presence of a stable dry season key resource areas such as the riparian zone which act as a buffer or rescue zones to cushion herbivores during the droughts.

Alternatively, during the rainy seasons, arid ecosystems exhibits a non-equilibrium relationship between the herbivore and forage supply in the sense that vegetation growth and forage supply in arid ecosystems such as RNP relies on rainfall and therefore there is usually an imbalance between animals populations and available forage during the wet season (Hempson *et al.*, 2015). The current study assessed how forage production in RNP vary with time, in seasons, and between landscapes and factors that regulates forage availability in this arid ecosystem. The study also assessed the role that the dry season key resource (riparian zone) play in regulating the equilibrium and non-equilibrium relationships between herbivores and forage supply in RNP.

Studies done in RNP have shown that grazing and trampling are highly concentrated at stock posts (Hendricks *et al.,* 2005b; Smet and Ward, 2006). Stock posts are designated residential points in the park where pastoralists settle with their animals (Figure 1.1 and Figure 3.4). Pastoralists are allowed to settle only in stock posts that are already established in the park (Hendricks *et al.*, 2005a). Studies done in NRP and in the larger Succulent Karoo biome (Anderson *et al.*, 2010, Hempson *et al*., 2015) have documented the effects that these settlements around the stock posts and watering points (piosphere effects) have on perennial plants but very little has been done on their effects on annual plants. This study therefore addresses the effects of grazing and abiotic factors such as rainfall on species richness, diversity and productivity of annual plants-dominated vegetation in Richtersveld National Park (RNP). The study is very crucial in assessing the drivers of vegetation change in this annual-dominated ecosystem in the Succulent Karoo. Of particular interest in the context of the pastoral system in the RNP is the increased productivity of annual plants near the stock posts, and whether the annual plants could to some degree compensate for the loss in canopy cover, diversity and productivity of that was reported by Hendricks *et al.,* (2005b) in RNP.

In order to have a win-win situation between pastoralism which is the main source of livelihood for the communities that live within and around RNP and on the other hand support the sustainable conservation of vegetation in this winter rainfall ecosystem, there is need to understand the various ecological dynamics that exists in this arid ecosystem. RNP is an arid winter rainfall region with highly variable rainfall and diverse vegetation composition and distribution across the landscapes (Mucina *et al.,* 2006). Spatial-temporal variation in rainfall and vegetation plus the presence of the perennial riparian zone, semi-nomadic pastoralists based at stock posts, and the context of a system where people are trying to reconcile pastoralist livelihoods and traditions with biodiversity conservation, makes this ecosystem more complex and therefore there is need to understand how all these factors are inter-related.

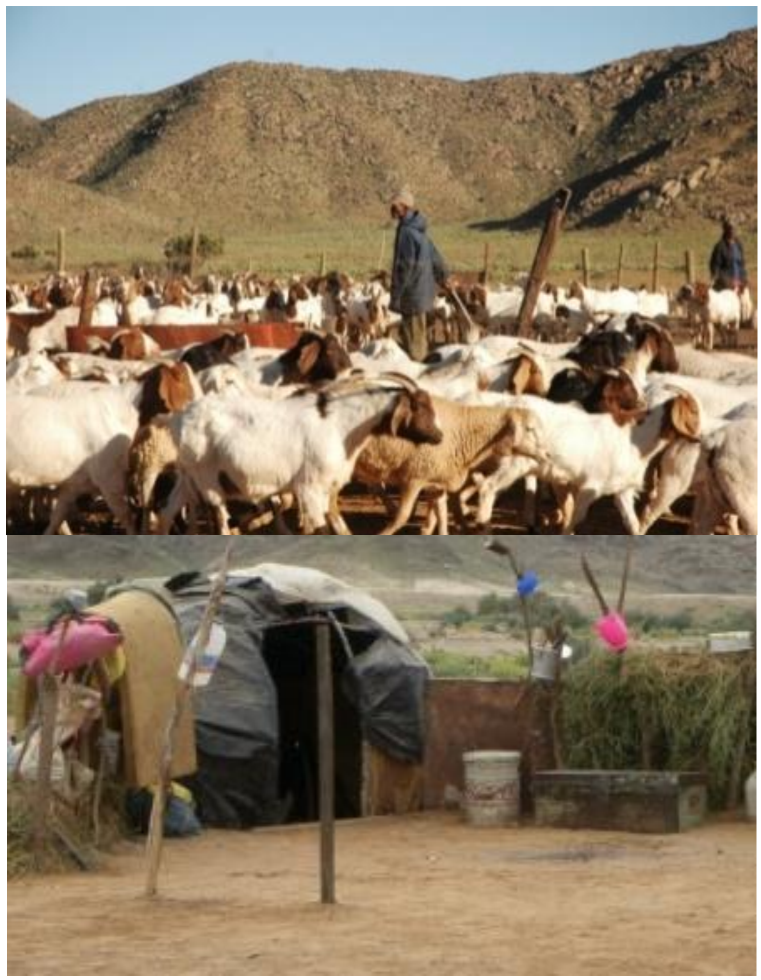


Figure 1.1: An example of a stock post in Richtersveld National Park
(Photo taken by Hempson *et al*., 2015)

Study on variation in forage production as well as the understanding of factors that influence forage variability in RNP will guide in development of adaptive management policies on pastoralism and biodiversity conservation in arid ecosystems. From pastoralism point of view, it is important to understand spatial-temporal variability in distribution of forage resources in RNP and how this heterogeneity together with integrated management systems would help to mitigate environmental degradation and animal loss.

The research intended to fill the knowledge gap on the effect of land use activities on dominant annual plants especially near the stock posts (piosphere effects). Piosphere effect is the negative impact that herbivores cause to plants around the stock post (Vetter, 2005). Such negative effects include; trampling, over-grazing and high concentration of animal dung and urine. The study will also address the implication of replacement of perennial plants with abundance of annual plants in arid ecosystems.

The study will assess the role of a stable dry season key resource in RNP in regulating equilibrium dynamics between dry and wet season forage resources. A wet season resources consists of annual herbs and perennial shrubs that herbivores depend on during the rainy season. On the other hand, a dry season resource (which is also referred to as a key resource) consists of forage available during the dry season mostly along the riparian zone of the large and perennial river or around established water points such as boreholes (Hempson *et al*., (2015). Equilibrium dynamics in arid ecosystems occurs when heavy grazing in rangelands negatively affects the vegetation growth and availability of forage.

Arid ecosystems such as RNP can have both equilibrium and non-equilibrium dynamics (Jakoby *et al*., 2015). In equilibrium systems, plants and herbivore populations are relatively tightly coupled, with grazing as a driving factor of plants growth, composition and productivity. On the other hand, disequilibrium dynamics also exist in many arid and semi-arid rangelands whereby vegetation growth and herbivore populations are more strongly driven by stochastic climatic factors such as rainfall than grazing (Hempson *et al*., 2015)

1.2. Statement of the Problem

Grazing is the main land use activity in RNP. Continuous grazing has led to loss of vegetation cover, replacement of palatable with unpalatable species, loss of perennial shrubs which are being replaced by annual plants as well as rangeland degradation (Anderson *et al.,* 2010). Rainfall patterns in RNP are also erratic and therefore forage production in this arid ecosystems is unpredictable. Abiotic factors such as rainfall in addition to land use practices such as grazing have been found to influence forage production and availability (Hempson *et al.,* 2015).

Studies done in RNP have concentrated more on effect of grazing on perennials plants (Hendricks *et al*., 2005b; Hempson *et al.,* 2015) and no study has been done on how biotic factors such as rainfall and abiotic factors (grazing, landform and soil variables) affect the annual plants. In addition, RNP is an ecosystem that is characterized by landscapes heterogeneity that ranges from flat plains, foothills and mountains. The ecosystem also has a riparian zone that herbivores depended on during the dry season. Due to the diverse landscapes heterogeneity, the forage production and distribution also vary with space and time. The study availed the lacking information on spatial and temporal forage variability in RNP that is vital to pastoralists and park manager, for effective rangeland management.

1.3 Justification

Little has been done on forage production, variation and distribution in RNP despite the fact that it is an arid ecosystem that has a distinct wet season resource landscapes and a large dry season resource (a key resource) along the Orange River riparian zone. Considering the landscape heterogeneity and climatic variability in RNP, the ecological study of spatial and temporal forage production in this arid ecosystem is important in the formulation of management plans, and conservation policies of this national park. The study helped to understand how forage production vary in RNP and what factors drives forage productions and distribution.

From a pastoral or herbivores point of view, it is of great importance to understand how availability and distribution of forage resources varies and how resource variation and heterogeneity help to mitigate environmental degradation and animal loss through utilization of different landscapes at different seasons. Study on variation in forage production as well as the effects of land use practices on vegetation will guide in development and implementation of adaptive management policies that can be applied in RNP as well as in conservation of other similar rangelands worldwide.

For better management and conservation of arid rangelands, it is advisable to understand the ecological factors that influence forage production and distribution in RNP as well as the significance of temporal and spatial heterogeneity in forage production in this arid ecosystem in order to effectively support the livelihoods of pastoral communities as well as to achieve sustainable environmental conservation. .

1.4 Research Questions

The research was guided by the following questions:

i) Which abiotic factors influence biomass production, species richness, diversity and composition of annual plants in RNP?

ii) Which biotic factors influence biomass production, species richness, diversity and composition of annual plants in RNP?

iii) Was there spatial and temporal variation in forage production by shrubs?

iv) What is the difference between the spatial and temporal variation in forage production in the dry season forage resource compared to the wet season resource and which factors drive forage heterogeneity in RNP?

v) What were the factors that influence forage production and variability in RNP?

1.5 Hypotheses

i) There is a positive correlation between abiotic factors especially rainfall, with forage production and distribution in RNP.

ii) Biomass production, species composition and diversity of annual plants are positively correlated with biotic factors, such as grazing, soil nutrients and landforms

iii) There is spatial and temporal variation in forage production by shrubs in RNP

iv) There is less spatial and temporal variation in forage production in the dry season key resource (riparian zone) than in the wet season resource areas

v) Abiotic factors influence spatial and temporal variation in forage production more than biotic factors.

1.6 Objectives

1.6.1 General Objective

To investigate the spatial and temporal variation in forage production and availability in the wet and dry-season resource areas of the Richtersveld National Park and the factors that influence forage production and variability.

1.6.2 Specific objectives

i) To assess the effects of abiotic factors (rainfall) on plant biomass production, species composition and diversity of annual plants in RNP.

ii) To assess the effects of biotic factors (grazing intensity, topography and soil nutrients) on plant biomass production, species composition and diversity of annual plants in RNP.

iii) To assess the spatial and temporal variation in forage production by shrubs.

iv) To quantify spatial and temporal variation in browse production by woody plants along the riparian zone

v) To determine the factors that influence forage production and variability in RNP

1.7 Significance of the Study

Despite being an arid ecosystem that is currently dominated by annual plants and with a long history of herbivores grazing, studies done in RNP have focussed more on perennial plants and herbivores (Hendricks *et al* 2004; 2005a; 2005b; Hempson *et al* 2015), very little has been done on annual plants and what drives their productivity, composition and distribution in this arid ecosystem. The larger Richtersveld area (where RNP is located) is generally regarded as one of the world's richest succulent ecosystem associated with the large succulent families, some of which are endemic to the area and thus need to be conserved (Mucina and Rutherfold, 2006).

Communal semi-nomadic pastoralism has been practised in RNP for decades, and livestock farming is an integral part of the economy and culture of the pastoralists who graze their animals (goats and sheep) in the park. Due to lack of policies that would regulate the number of animals to be domesticated as well as the movement of pastoralists in the park, overgrazing in this communal rangeland is likely to occur (Hendricks *et al.*, 2004). The establishment of RNP as a contractual park between the local communities and the South Africa government aimed to conserve the rich biodiversity found in RNP and at the same time take care of the interest of the pastoralists living in the park. So there was need to reconcile pastoralism for the sake of communities that rely on herbivores as source of livelihood and conservation of the rich biodiversity found in RNP. To neutralize the negative effects associated with over-grazing, it is important to understand spatial-temporal variation in forage production in RNP, factors that drive forage heterogeneity and distribution in this ecosystem and advocate for resource partitioning as one of the management strategy.

The study on spatial and temporal forage availability and distribution is of benefit to pastoralists and park managers as it sheds light on where and when the forage is available at different time and seasons of the year. Studies on the effects of biotic and abiotic factors on forage production in RNP is appropriate to understand the drivers of vegetation growth in this ecosystem. The study will bring out the role of a large and stable dry season key resource such as riparian zone in arid rangelands, not only in RNP but worldwide. Understanding the role of a key resource areas and landscape resource variability supports protection of critical forage hot spots for herbivores.

1.8 The structure of the thesis

This thesis is organized in 7 chapters as follows:

Chapter 1: This chapter introduces the study and presents the background information, context of the study area, the research gaps, hypothesis and objectives.

Chapter 2: Literature review dealing with the broad issues

Chapter 3: Describes the study area, materials and methods

Chapter 4: This chapter deals with objective 1 and 2 (forage production by annual plants in RNP and the biotic and abiotic factors that influence the annual plants in RNP)

Chapter 5: This chapter deals with objective 3 (on spatial-temporal variation in forage production by shrubs in RNP)

Chapter 6: This chapter deals with objective 4 and 5 (Spatial and temporal variation in browse production by trees and grass species along the riparian zone in RNP)

Chapter 7: Synthesis of all the above findings with a conclusion and recommendations on the best practices in terms of pastoral system and biodiversity conservation in RNP.

Bibliography (references)

CHAPTER 2: LITERATURE REVIEW

2.1 Equilibrium versus disequilibrium dynamics in rangelands

There has been debate on what influences vegetation growth and herbivores in arid rangelands. Many studies have championed the existence of equilibrium dynamics in arid ecosystems, whereby heavy grazing in rangelands has been reported to have a negative impact on vegetation cover, biomass production and plant species diversity and composition. For example, van Rooyen *et al.,* (2015), showed that plant canopy cover increased with withdrawal of livestock grazing and inferred that animal density affected primary produ ction. Todd and Hoffman (2009) also reported negative effect of grazing on biomass production of perennial plants in South Africa rangelands.

In equilibrium systems, plants and herbivore populations are relatively tightly coupled, with grazing as a driving factor of composition and productivity. The effects of this are often especially pronounced after a prolonged drought due to decline in vegetation growth. In contrast, some studies show that disequilibrium dynamics also exist in many rangelands whereby plants growth and herbivore numbers were found to be more strongly driven by unpredictable climatic factors such as rainfall than grazing (Hendricks *et al.,* 2005b; van Rooyen *et al.,* 2018). In systems where disequilibrium dynamics predominate, the abiotic factors mainly rainfall results in imbalance between plants growth and herbivore numbers and therefore they rarely reach equilibrium because of fluctuating supply of forage resource (Vetter, 2005). Hempson *et al.,* (2015) argue that many semi-arid rangeland systems are not at equilibrium much of the time, but nevertheless exhibit equilibrium dynamics with that part of the resource which limits the herbivore populations during the period of greatest forage scarcity. Herbivore populations are in equilibrium with this subset of the key resource, while being largely uncoupled from the bigger, but seasonally unavailable, wet season resource.

Unlike perennial plants that are greatly affected by grazing, the composition and abundance of annual plants has been found to be more strongly influenced by rainfall from year to year (van Rooyen *et al.,* 2018). A strong positive relationship between composition, diversity and productivity of annual plants and rainfall have been reported in arid ecosystems such as Succulent Karoo (Schimiedel *et al.*, 2012), in the Nama Karoo (van der Merwe *et al.*, 2018) as well as in other arid ecosystems (Yan *et al.,* 2015).

For better management and conservation of arid rangelands, it is important to understand the ecological implications resource heterogeneity in order to support the livelihoods of pastoral communities as well as to achieve sustainable biodiversity conservation (Salmon *et al.*, 2013). From a pastoral or herbivore point of view, it is of great importance to understand how availability and distribution of forage resources varies and how the resources heterogeneity can help to mitigate environmental degradation and livestock loss through utilization of different landscapes at different times of the year. Pastoralists make use of spatial heterogeneity as forage resource and rainfall patterns are not uniform across the landscapes (Samuels *et al*., 2013). Spatial heterogeneity therefore acts as a buffer to rainfall and forage variability.

2.2 Spatial-temporal resource heterogeneity in rangelands

In South African rangelands, variation in forage production at any scale has been overlooked in pastoralism management plans for a long time, and movement restriction systems (in paddocks) were imposed based on traditional rotational grazing systems commonly used on commercial farms (Baker and Hoffman, 2006). Such management practices were found to be ill-suited to the landscapes and resources variability that characterize African rangelands (Samuels *et al.*, 2007). It has been observed that when livestock make use of diverse ecosystems and landscapes, their impact on vegetation in terms of over-grazing, trampling and alteration of species composition is reduced due to the time of rest and re-growth given to the vegetation (Fynn, 2012).

Grazing intensity in most of rangelands is not evenly distributed due to uneven distribution of water and forage resources, as well as settlement patterns of the pastoralists. For example, Nsinamwa *et al*, (2005) observed an uneven utilization of herbaceous plants by livestock. This has been reported in other studies where grazing is more concentrated in preferred areas known as ‘foci’ points or piosphere (Savadogo, 2007)). These foci points include areas around watering points, pastoral campsites, villages and stock posts.

Previous research indicate that species diversity, richness and biomass production of herbaceous species are low near foci points and increase with distance away from them (Savadogo, 2007; Tefera, 2013). Hendricks *et al.,* (2005a), also found that species diversity and richness of perennial shrubs increased with distance away from the stock posts. This is due to high grazing and trampling impact by herbivores as they flock to drink water (around watering points) or rest every evening in the stock posts. From management of rangelands point of view, due to the observed piosphere effects on plants and soils around watering points and settlement points, establishment of additional stock posts should be discouraged and herbivores should not be concentrated at one particular point for long period of time (Nsinamwa *et al.,* 2005) . Also rangeland managers need to regulate the movement patterns and herd sizes especially in enclosed ecosystems such as RNP.

2.3 Plant-herbivore dynamics in RNP

In arid ecosystem where pastoralism is among the main land use activities, there exists a direct relationship between the forage availability and herbivore dynamics (Fynn, 2012). Hempson *et al.,* (2015) also noted that goat populations in RNP were regulated by the availability and depletion of forage along the Orange River riparian zone during the dry season, consistent with the theory that herbivores are at equilibrium with their key resource (Hempson *et al.*, (2015). This was due to depletion of tree foliage from the ground up to a browse line of 1.5 metres (accessible by goats). Forage depletion was positively correlated with goat densities and the length of time goat populations spent in the riparian zone (which in turn depended on the timing of the onset of the first rains). In contrast, the goat populations were largely uncoupled in their dynamic from the wet season resource (the plains, foothills and mountainous landscapes away from the Orange River).

Hendricks *et al.,* (2005b) argued that the reason pastoralists moved their goats to the dry season resource areas along the Orange River at the beginning of summer was because of high temperatures on the plains and the demand for water for herbivores. This illustrates that animal densities were not limited by shortage of forage during the rainy season, indicating presence of disequilibrium dynamics during the wet seasons. This clearly show that Richterveld National Park exhibit multi-equilibrium state (both equilibrium and disequilibrium dynamics) at different seasons and landscapes in a year.

In RNP, the presence of a key resource (the Orange River riparian zone) can have both negative and positive impacts. In a drought season, the availability of a key resource would help to prevent economic losses by reducing deaths of livestock by providing forage during the drought. Alternatively, this can cause negative environmental impact due to degradation of rangeland as a result of overgrazing.

2.4 Measurement of forage productivity in rangelands

There is a difference between measurement of biomass production and primary productivity in rangeland ecosystems. Biomass is the total standing biomass out of cumulative Net Primary Productivity (NPP) over time while NPP represents the amount of organic material produced by a plant. In terrestrial ecosystem it is often difficult to measure primary productivity because a substantial proportion of total productivity is shifted to below ground organs and tissues where it is difficult to measure. Various methods have been used to measure primary productivity but most of them have some limitations such as size of the area that can be covered, costs implication, time taken and accuracy of the methods used (Easdale and Aguiar, 2012).

The harvest method has been widely used in the past due to unavailability of technological skills and know-how on use of remote sensing data (Eisfelder *et al.,* 2014) but it is laborious, expensive and destructive and can only be done over limited spatial scales. The alternative, less intensive methods of measuring primary productivity that have been widely used include remote sensing and use of allometric relationships between readily obtained plant measures (such as plant height, canopy area, cover, leaf area index, stems length and diameter) with biomass (Eisfelder *et al*., 2014; Hempson *et al.,* 2015). To allow accurate prediction of biomass production from these more readily measured proxies, it is essential that these are calibrated by actual measurements of above-ground net primary production (ANPP). All these techniques require calibrations before they can be used for specific situation.

Primary productivity in rangelands can also be estimated by the use of remote sensing techniques, whereby primary productivity is determined by the amount of photosynthetically active radiation (PAR) absorbed by the plant canopy (Palmer and Yunusa, 2011; Hempson *et al.,* 2015). The advantage of using satellite remote sensing to estimate Net Primary Productivity (NPP) is that a large area can be measured directly without harvesting the vegetation, but calibration is required through ground-truthing. Use of low (1 km^2) Spatial Resolution Satellite Data such as MODIS imageries collected at high frequency make it possible to track productivity changes and habitat quality at a smaller scale with possibilities of going back in time and covering a large area within a short period of time (Eisfelder *et al.,* 2014). Remote sensing data on primary productivity has been widely used in measurement of forage production in arid rangelands (Eisfelder *et al.,* 2014). The technique was useful in this study as it helped in measurement of primary productivity in areas of the park that are not easily accessible such as in the mountains and steep valleys.

2.5 Management and conservation of heterogeneous arid rangelands

Pastoralism, characterized by animal movements between different landscapes to search for forage and water resources has been the successful survival strategy for most pastoralist in most rangeland ecosystems (Kimiti *et al.,* 2018). In East African rangelands, studies have shown that due to changing land tenure and increased human settlement in the rangelands there has been restricted livestock mobility resulting in sedentary pastoralism that exerts pressure to vegetation thus leading to range degradation (Notenbaert *et al.,* 2012; Kimiti *et al.,* 2018). Restricted animas and human mobility has led to overgrazing in the fragmented rangelands, thus causing decline in rangeland productivity which was evidenced by low biomass production (Western *et al.,* 2015).

Continuous grazing by herbivore due to restricted movements result in decline in range productivity, low land carrying capacity, low soil fertility, and eventually range degradation and desertification (Notenbaert *et al.,* 2012). Appreciating the responses of livestock to heterogeneity of vegetation resource is vital in the management of arid rangelands (Samuels *et al.,* 2019). For example, in South African, the introduction of movement restriction systems in form of paddocks was found to be unsuitable to the sustainable utilization of complex and variable rangelands. This was because there was no flexible movement of animals to track the heterogeneous range resources (Fynn, 2012).

More flexible and adaptive rotational grazing and resting guided by the variations in forage production in space and time is considered more appropriate in these heterogeneous and unpredictable systems. Mobility of livestock enables efficient utilization of heterogeneous rangelands at different times of the year as well as in preservation of landscapes as refugia or reserves for forage to be used during the dry periods (Tefera, 2013). Mobility during drought is very crucial for survival of herbivores (Samuels *et al.*, 2007).

The study was expected to fill the knowledge gap on spatial and temporal variation in forage production and availability during the wet and dry seasons in Richtersveld National Park. Additionally, to determine the factors that influence forage production and variability in RNP. Of great importance was to find out the effect of biotic and abiotic factors on annual plants and on spatial and temporal resource heterogeneity in the park. The study will also conceptualize how the findings can be applied in the management and conservation of arid ecosystems globally.

2.6 Conceptual framework

The conceptual framework of the study was well illustrated in Figure 2.1. The framework shows how the abiotic factors (rainfall) and the biotic factor (grazing intensity, land forms and soil nutrients) affects the annual and perennial plants in RNP. The conceptual framework shows relationship between the independent (biotic and abiotic) factors and the dependent factors (species richness, species diversity, biomass production, forage availability, biomass production, forage heterogeneity and forage availability) and eventually the herbivores which rely on plants. On the other hand, high herbivore populations' leads to overgrazing that cause decline in vegetation cover, plant biomass, richness and diversity.

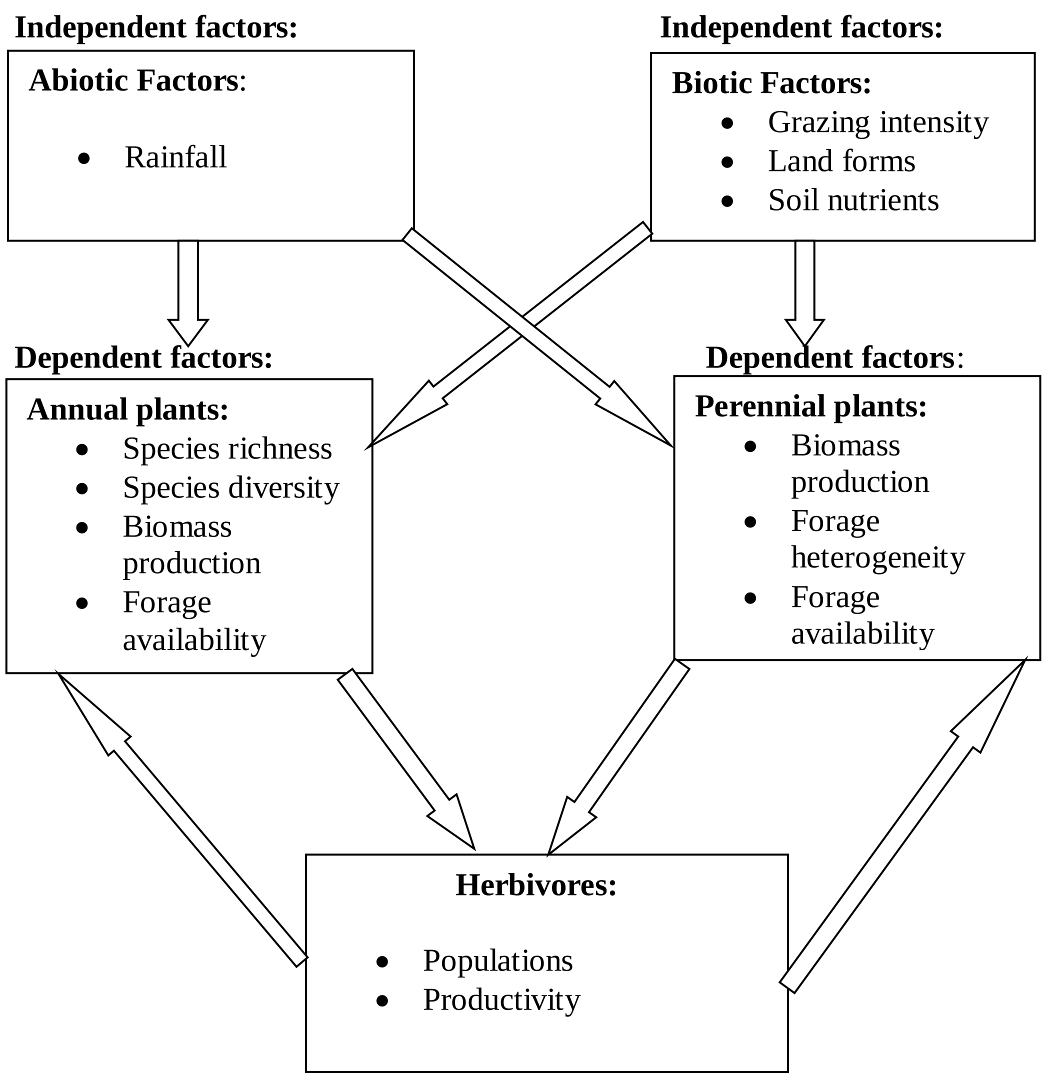


Figure 2.1: The conceptual frame work

CHAPTER 3: STUDY AREA, MATERIALS AND METHODS

This chapter describes various aspects of the study area, Richtersveld National Park such the geographical location, biophysical features, climate, vegetation types and land use activities in the park. The materials and methods of data collection were well described in respective chapters per objective in chapter 4, 5 and 6 to avoid repetition.

3.1 Geographical location and institutional setting

The Richtersveld National Park (RNP) is located in Namaqualand, north-western South Africa, (28° 15' S, 17° 10' E) shown in Figure 3.1. The park is 162,445 ha in land size. The succulent karoo biome is globally recognised as a biodiversity hotspot and is associated with endemism of wide range of faunal and floral groups, with 30% of the world's succulent species found in the area (Mucina *et al*, 2006). RNP is a contractual park that is managed jointly by South African National Parks (SANParks) and the Richtersveld pastoralist community who lived in the area before the park was licensed in 14^{th} August 1991.

Semi-nomadic pastoralism has been practised by the Nama people in the Richtersveld for about 2000 years (Hendricks *et al.*, 2005a). The RNP has a long history of the negotiations between the local pastoralists and the South African National Parks (SANParks) with an aim to conserve the rich biodiversity found in this area. Pastoralism is the main source of livelihood of the Nama people. It plays an important role in the household economy of the Nama community. Livestock usually supply meat, milk, hides, pelts and income for the Nama community. The livestock industry of the Richtersveld comprises mainly of Boer-goats and some sheep, grazed as a mixed herd.

The Nama people living in Richtersveld are economically inactive inhabitants of this region. Their incomes are low and they solely rely on pastoralism. A trade market of animals does not exist, and they mostly trade among themselves. The Nama pastoralists in Richtersveld constitutes traditional communal grazing land with distinctive semi-nomadic nature of livestock management. None of the pastoral families have permanent residence within the park, but they have permanent homes in the villages surrounding the park (mostly where women, children and elderly men live).

According to Hendricks *et al.,* (2004) proper management strategies should be effected in the RNP to strike a balance between the conservation efforts and pastoralism which is the main land use activity. Reduction of herd sizes was not a popular option according to pastoralists and therefore restricting herd movement to some landscapes was seen to be much responsive strategy than reducing the livestock numbers (Hendricks *et al.,* 2005a). Fencing of the prohibited landscapes that had threatened species was found not to be a suitable conservation strategy because of the presence and movement of tourists in RNP. Partitioning of the RNP into different zones according to specific land use activities was seen to be a suitable intervention. Other conservation interventions that were suggested by (Hendricks *et al.,* 2005b) include the closure of stock posts located in landscapes that were considered to be of high conservation priority. All these initiatives were meant to reconcile the efforts towards conservation of plant species and pastoralism NRP.

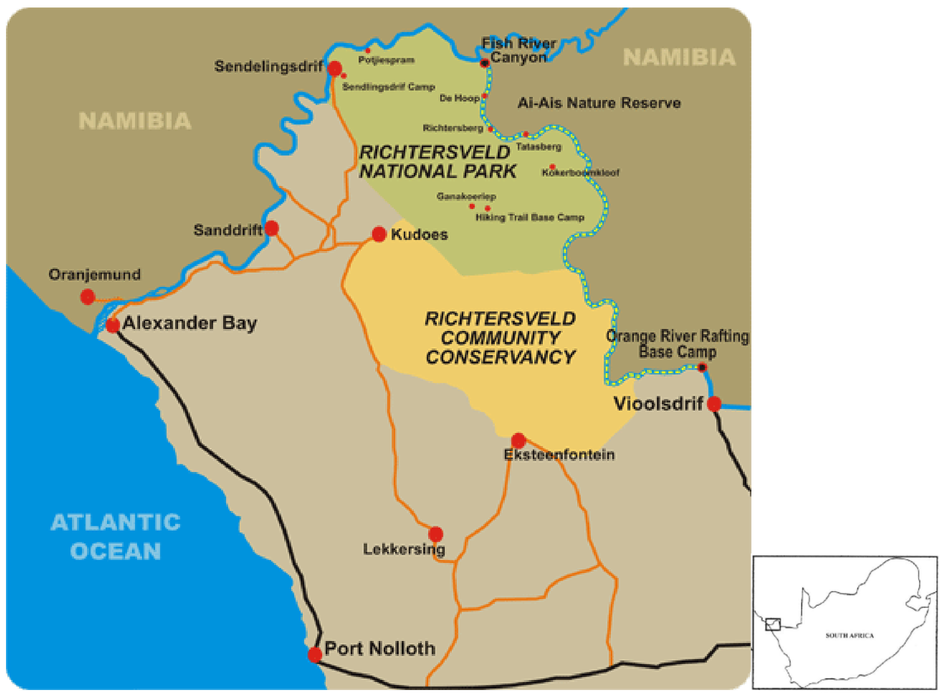


Figure 3.1: Map of Richtersveld National Park within the larger Succulent Karoo in South Africa (**Source**: Mucina and Rutherfold, 2006)

3.2 Biophysical aspects (topography, geology and soils) in RNP

Richtersveld is regarded as one of the most unique mountain desert in South Africa (Mucina and Rutherfold, 2006). The park has unique mountainous terrains, deep valleys and gullies that stretch out into the Orange River beds. Four major land types can be identified in the RNP namely: the Orange River flood plains, gently undulating planes, the rolling hills and the rugged mountains. According to (Mucina and Rutherfold, 2006) are mainly three plains in the RNP. These are the Koeroegabvlakte, Springbokvlakte and the Rooilepel.

The geology of the park and immediate surroundings is underlain by rocks. Succulent Karoo soils are well suited to favour diverse plant species due to nutrients supply from the continuous weathering and mineralization process (Mucina and Rutherfold, 2006) and sub-surface water storage and supply to plants. Perennial vegetation shows strong patterning with high plant turn-over related to soils and geology, as it typical all over the succulent karoo.

3.3 Climate of the study area

RNP is an arid winter rainfall area, with high rainfall variability. It has a mean annual rainfall ranging between 52 mm in the desert parts, 102 mm in the lower lying central plains, to 248 mm in the mountainous parts of the interior. Temperatures varies between 14^{o}C - 25^{o}C in June and can rise to above 50^{o}C in the summer and drop to 0^{o}C on winter nights. There are five rain gauges in the park, one in each vegetation type as shown in Figure 3.2. Rainfall data is usually recorded daily during the rainy seasons and forwarded to South Africa Weather Service offices located in Pretoria.

The climate of Richtersveld is characterised by a short winter rainfall season (4 months) and a long dry summer season (8 months) annually. The largest western and central part of Richtersveld received short winter rainfall in form of soft, gentle rains usually from late April to September with peaks in May and July in a year. On the other hand, the eastern part towards the Orange River receives summer rainfall between October and April that is usually in form of thunder-showers which last for a very short period. The RNP is characterised by relatively high wind speed that range between 7km/hr in January and 4km/hr in June (Hempson *et al.*, 2015).

3.4 Vegetation types and biomes in RNP

There are two vegetation biomes in RNP namely; the succulent karoo biome and the desert biome. Succulent karoo biome is found on the western and central parts of RNP, while the desert biome is on the north-eastern, eastern and south-eastern part of the park (van Rooyen *et al*., 2015). The succulent karoo biome forms the major part of the Richtersveld Mountains that are steep and rocky (Mucina *et al*., 2006). The succulent karoo part of the park receives winter rainfall between late April to late August and rainfall varies from 80–250 mm per annum (Palmer *et al*., 2011). At higher altitudes, especially on south-western slopes, occurrence of fog results in a significant improvement in water supply that support diverse plants species in the area (Palmer *et al*., 2011)

On the other hand, the Desert Biome has sparse shrubby vegetation in some places (Hempson *et al*., 2015). Soils are very shallow and patchy. Deeper and more developed soils are formed in cracks and crevices in places that receive larger amounts of summer rainfall runoff. Rainfall seasonality has transitional features between winter and summer, and is poorly predictable. High temperatures in summer are common. Fog does not play an important role in the dry desert biome.

There are five vegetation types in RNP. These are (i) Central Richtersveld Mountain (ii) Northern Richtersveld Scorpionstailveld in the succulent karoo biome (iii) Noms Mountain Desert, (iv) Richtersberg Mountain Desert and (v) Richtersveld Sheet Wash Desert found in the desert biome (Mucina and Rutherfold, 2006) as shown in Figure 3.2. On the other hand, vegetation types found in the Desert biome experience very low winter rainfall and relatively higher temperatures compared to the western mountains of the succulent karoo biome. Sometimes erratic summer rainfall also occurs in the desert biome. Dwarf shrubs and grass species are common in the vegetation types found in the Desert Biome.

The vegetation of the RNP was composed of variety of leaf and stem succulents of the family Aizoaceae, woody shrubs, diverse annual plants and geophytes, succulent shrubs being the most distinctive family in the succulent karoo (Mucina *et al.*, 2006). Various plant growth forms found in RNP are shown in Figure 3.3. Trees and grasses occur mainly along the Orange River riparian zone (Figure 3.3c-d). Other dominant plant families are Euphorbiaceae, Crassulaceae, Asteraceae, Iridaceae, and Hyancinthaceae (Mucina and Rutherfold, 2006). Unpalatable plants such as *Mesembryanthemum guerichianum* (Aizoaceae), *Mesembryanthemum barkiyi* (Aizoaceae) and *Galenia africana* (Aizoaceae) dominate areas around the stock posts which are characterised by heavy grazing, high concentration of dung and urine and animal trampling (Hendricks *et al.*, 2005a).

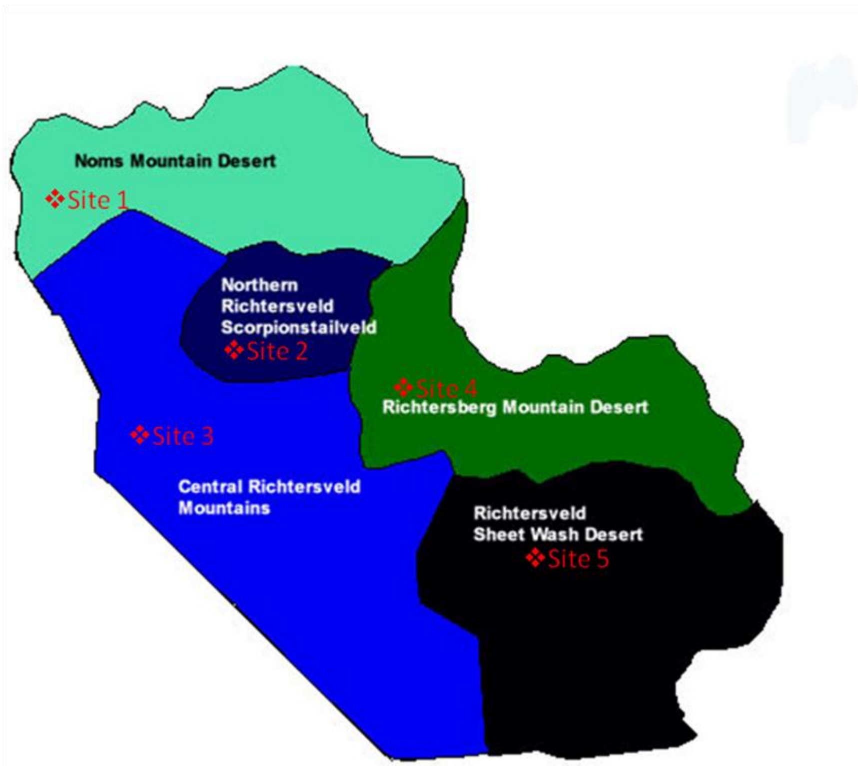


Figure 3.2: Map of the study area showing the 5 vegetation types and study sites. (Source: Mucina and Rutherfold, 2006)

3.5 Land use (pastoral system) in the park

In the larger Richtersveld grazing land is still under the system of communal land ownership (Hendricks *et al.*, 2004). Communal land ownership is based upon membership and a series of rights and duties with respect to the use of the land.

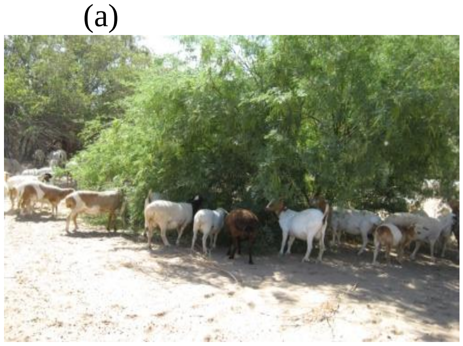
Each pastoralist has the right to access the communal grazing areas which provides forage and water for their goats and sheep. Grazing arrangements was by consensus among the pastoralists. There was also no formal rules to regulate the movements or the number of goats and sheep to be kept on the communal land outside the park. However, a different tenure arrangement exists in RNP. The South Africa National Parks (SANParks) initiated a 30 year lease in 1991 with the Nama community with the aim of conserving the biotic diversity and to manage the communal grazing resources within the park in cooperation with the local communities.

The original inhabitants of 26 households living within RNP, had agreed to maintain the number of livestock grazing in the park to a total of 6600 goats and sheep kept by all the 26 registered households living in the park (Hempson *et al*., 2015). The carrying capacity was based on the approved stock carrying capacity by National Department of Agriculture of 25 hectares per small stock unit. Under this agreement, pastoralists were also expected to settle with their animals only in the established stock posts and they were discouraged from creating new ones (Hempson *et al*., 2015).

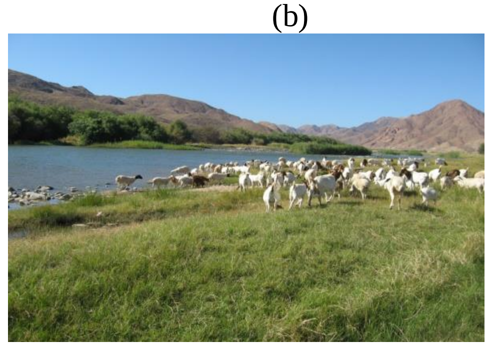
The pastoralists (Nama people) graze their livestock (mainly goats and sheep) in the park, and they move between stock posts at varying intervals in response to forage and water availability (Hendricks *et al*, 2004). Stock posts are designated semi-permanent residential points in RNP where pastoralists settle with their animals, and after day long grazing, they return with their animals to these resting places overnight. Figure 3.1 shows an example of a stock post. There are 26 registered pastoralists (households or family units) whose rights to graze livestock in the park are recognised, and 270 stock posts have been established in the park over time (Figure 3.4).

(a)

(b)



(c)



(d)

Figure 3.3a-d: Different vegetation growth forms found in RNP

In Figure 3, plate (a) shows the herbaceous annual plants and (b) the succulent shrubs photographed during the wet season in the Succulent Karoo vegetation types, (c) the trees and (d) the grasses providing forage year-round in the riparian zone of the Orange River. The flocks of livestock consist primarily of Boer goats and some sheep. In addition to goats and sheep, other animals found in RNP include; klipspringers *Oreotragus oreotragus* (Zimm.), desert rats *Petromus typicus (*A. Smith), grey rhebok *Pelea capreolus* (Forster), cape porcupines *Hystrix africaeaustralis* (Peters) , jackals *Lapulella mesomelas* (Schreber), spotted hyenas *Crocuta crocuta* (Erxleben), leopards *panther pardus* (Linnaeus) and shrews *Myosorex varius* (Smuts) though they are few in numbers. The few wild herbivores found in RNP include; mountain zebra *Equus zebra* (Linnaeus), small insectivores, shrews *Myosorex varius* (Smuts), horse-shoe bats *Rhinolophus damarensis* (Roberts), monkeys *Chlorocebus pygerythrus* (F. Cuvier) and Chacma baboons *Papio ursinus* (Kerr.). Their effect on plants is very minimal because they are very few in numbers (Hempson *et al*., 2015).

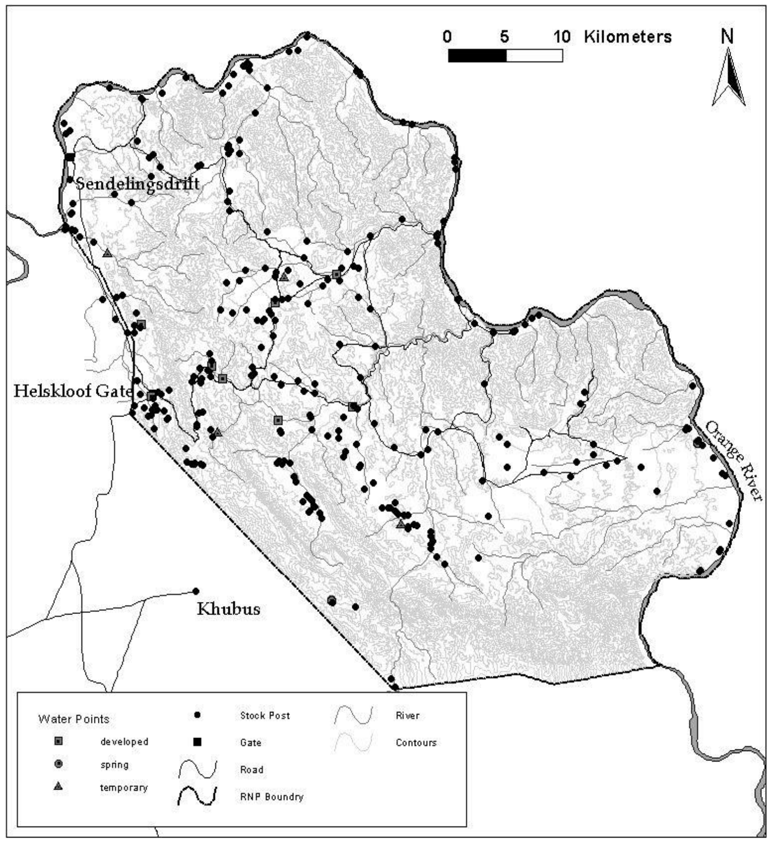


Figure 3.4: Distribution of stock posts (black dots) in Richtersveld National Park (Source: Hendricks *et al*. 2005a)

CHAPTER 4: EFFECT OF BIOPHYSICAL FACTORS ON ANNUAL PLANTS IN RICHTERSVELD NATIONAL PARK

4.1 Introduction

This chapter answers the research question on which biotic and abiotic factors drives the biomass production and composition of annual plants in Richtersveld National Park. The chapter also attempts to determine the role of annual plants in provision of forage during the wet seasons, the ecological impacts of the establishment of stock posts in the park, as well how equilibrium and non-equilibrium dynamics plays out in this annual dominated ecosystem.

4.2 Effect of biophysical factors on annual plants in arid rangelands

Rangelands are generally regarded as ecosystems in which primary productivity is controlled by herbivore density with a pattern of negative feedback which eventually produces a long-term equilibrium between plants and herbivores (Deng *et al.,* 2013). It has however been argued that in arid rangelands stochastic abiotic factors such as precipitation, have a greater influence on primary productivity and plant species composition than grazing (Tefera, 2013; Saayman *et al.,* 2016). This is due to the fact that plant production in arid areas depends on rainfall which regulates their growth and abundance (Sassi *et al.,* 2009). Studies have shown that both grazing and precipitation affects vegetation composition, richness, cover and production in rangelands (Rutherfold and Powrie, 2010), with abiotic factors generally playing a more important role especially where the vegetation is dominated by annual plants, or in influencing the annual component of the vegetation (van Rooyen *et al.*, 2018).

In Succulent Karoo, continuous grazing has been found to cause replacement of perennial plants with annual plants (Gilson and Hoffman, 2007; Schmiedel *et al.*, 2012) and composition, cover and diversity of perennials have been found to be influenced by grazing (Hendricks *et al.*, 2005a; Rutherfold and Powrie, 2010). In contrast, vegetation change of annual plants in Succulent Karoo was found to be influenced more by climatic factors such as rainfall than by grazing pressure (van Rooyen *et al.*, 2018). According to van Rooyen *et al.*, (2015; 2018) species composition of annual plants is determined by amount of rainfall during winter period and annual plants are influenced to the annual rainfall variability.

Rainfall patterns were found to influence annual plants through rapid seeds germination immediately after onset of rains, rapid growth, production and phenology that favors their short life cycles (Schmiedel *et al.*, 2012). Annual plants have been found to be unreliable source of forage in arid areas due to the effect of droughts that characterize the dry ecosystems and due to their short life span as there is very little carryover of forage from one season to another unlike in the case of perennials plants (Rooyen *et al.*, 2018). This observation implores the question of sustainability in forage supply in annual plants-dominated rangelands such as RNP, where perennial plants are being replaced by annual plants as a result of continuous grazing pressure.

Variability in stochastic abiotic factors such as rainfall influence forage availability in dry areas (Saayman *et al.*, 2016) which are characterized by short growing seasons, high frequencies of drought and great intra and inter-annual rainfall variability, which results in seasonal variations of primary production between the years (Sassi *et al.*, 2009; Jeddi and Chaieb, 2010). This is particularly true for annual-dominated vegetation because the biomass of annual plants is strongly rainfall-driven (Gillson and Hoffman, 2007).

4.3 Piosphere effect in RNP

Piosphere are areas around the stock posts where livestock are concentrated every evening. In the vicinity of the stock posts and watering points, herbivores create degraded areas known as piospheres (Shahriary *et al.*, 2012), whereby grazing, trampling, dung and urine are highly concentrated (Tefera, 2013). Other points considered as piosphere include areas around pastoral campsites and villages where animals aggregate in the evening (Figure 4.1). The piosphere effects on vegetation have been reported widely in African rangelands (Nsinamwa *et al.*, 2005; Smet and Ward, 2006; Tefera, 2013) in Botswana, South Africa and Swaziland respectively. The grazing gradients caused by these piospheres have adverse impact on plants composition, richness and biomass production

(Hendricks *et al.*, 2005a). Piosphere effect on perennial shrubs diversity, richness and productivity have been reported in several studies that were done in South Africa (Hendricks *et al.*, 2005b; Tefera, 2013) as well as in desert in Iran (Shahriary *et al*., 2012) but very few studies have been done on their effect on annual plants. There is need therefore to study the effect of grazing and soil nutrients on annual plants and to determine what drives the biomass production and composition of annual plants in Richterveld National Park.

Studies done in South Africa Succulent Karoo have shown the effect of rainfall variability on plant communities (Anderson and Hoffman, 2007) as well as on properties of soils (Petersen *et al.*, 2004). Annual plants have been found to be very productive during wet seasons and provide high quality forage but are strongly influenced by rainfall (Gillson and Hoffman, 2007). During drought periods annual plants do not germinate at all and therefore they turn out to be an unreliable source of forage (Sassi *et al.*, 2009; Tefera, 2013). Although annual plants are an important, though variable source of forage for herbivores in the Succulent Karoo, there is little information available on the effect of grazing and abiotic factors on the composition, diversity and primary productivity of annual plants in RNP. Of particular interest in the context of the pastoral system in the RNP is whether there is increased productivity of annual plants near stock posts, and whether this could to some degree compensate for the supply of forage resource at the expense of diminishing perennial plant cover and productivity. This study is very important in the management of rangelands in Succulent Karoo as it will investigate the piosphere effects on biomass production of annual plants.

The aim of this study was to assess the effect of rainfall, soil nutrients, land forms and grazing on composition, richness, composition and biomass production of annual plants in Richtersveld National Park. It was predicted that the annual component of the vegetation would respond most strongly to abiotic drivers with relatively little effect of grazing, and as part of the wet season resource. It was predicted the dynamics of annual plants to conform most strongly to the disequilibrium model. In addition, species richness, diversity and biomass production of annual plants were expected to be higher with higher rainfall, on the less accessible and rockier foothills, and with lower grazing pressure further away from the stock posts.

The study predicted increase in soil nutrients such as nitrogen, phosphorus and salts closer to the stock posts as a result of livestock dung and urine deposition. Given the ephemeral nature of the annual plants and the high rainfall variability of the Richtersveld, it was expected the composition of annual plants to be more strongly influenced by rainfall and soil conditions than by grazing intensity; and given the climate and vegetation differences between the desert and succulent karoo biomes, It was expected the annual communities to differ between the two biomes.

4.4 Methods of Data Collection

4.4.1 Determination of biomass production, species richness and diversity of annual plants

Sampling of annual plants was stratified by the five vegetation types found in RNP. Five sampling points were selected (one in each vegetation type) based on the following criteria (Figure 4.1):

a. Proximity to an occupied (by pastoralist and livestock) stock post. A stock post is an established place where pastoralists temporarily settle with their animals as shown in Figure 3.4.
b. Proximity to a rain gauge (There is a rain gauge in each of the 5 vegetation types.)
c. Occurrence of both foothill and flat plains close to the stock post, so as to assess the effect of landscape position on plant species (Figure 4.2a).

In total 60 stock posts were sampled, six sample plots per vegetation type (five vegetation types) and transects were laid in two landscapes (flat plains and foothills) as shown in Figure 4.2. At each of the five sampling sites, two 1000 m transects were laid from the center of the stock post, one on sandy plains and one on rocky foothills. Sampling was done at 3 distances from each sampled stock posts (100 m, 500 m and 1000 m) as described by Hendricks *et al.*, (2005b) to represent a grazing intensity gradient (Figure 4.1). Vegetation sampling took place four times at each sampling point, twice per year (July and September 2006 and 2007).

Mobile exclosures (steel cages covered with wire mesh, covering an area of (1 x 1m) were placed at each sampling point to exclude grazing, thus allowing primary production to be quantified. At each harvesting date, all annual plants inside the exclosures, and in adjacent 1 m^2 plots outside the exclosures were clipped to determine the amount of biomass removed by grazing (Figure 4.2b). Clipping was done in July and September (winter and early springs) to ensure that annual plants that germinated immediately after the onset of winter rainfall as well as those that germinated later in the growing season were captured. Clipped annual plants in each sample plot were identified, separated into different growth forms, recorded and then packed in polythene bags and were taken to the laboratory to be oven-dried and weighed for biomass. Exclosures were put in place before the onset of the winter rains and relocated after the first sampling in July to a place where no previous harvesting had taken place.

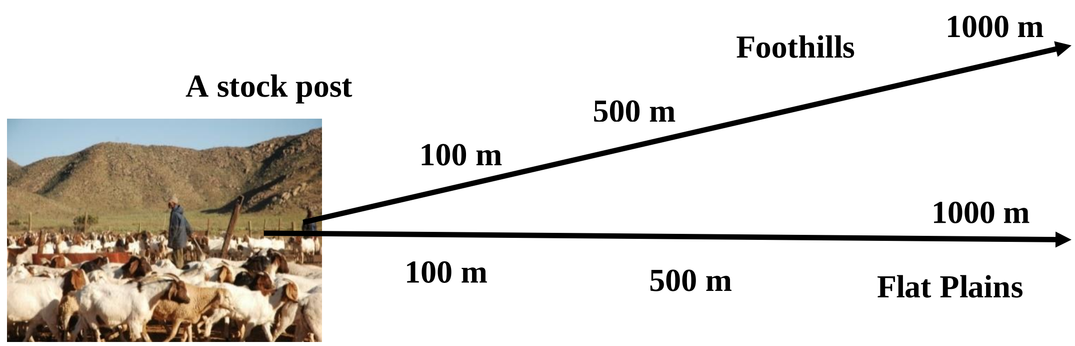


Figure 4.1: Sampling of annual plants in foothills and flat plains (the piosphere)

(a) (b)

Figure 4.2: (a) Different landforms in RNP (b) A 1 x 1 m plant exclosure

Figure 4.2 show the flat plains in the foreground where goats are grazing, and the steeper foothills in the background. (b) One of the 1m x 1m mobile exclosures used to exclude grazing in the sample plots.

4.4.2 Soil sampling and determination of soil properties

Soil samples were collected at the sites of each exclosure (N = 30) in September 2007. Four soil samples were collected from each sampling plot at a depth of 15 cm (Jeddi and Chaieb 2010), mixed and placed in a polythene bag. Soil samples were dried at 30º C for 12 hours. The soil analyses were conducted at BemLab laboratory (Stellenbosch, South Africa).

The following analyses were carried out for each soil sample:

a. Soil pH was determined electrometrically using a Cyberscan digital (pH 500/MV/ºC) bench pH meter.

b. Exchangeable bases (sodium and potassium) were determined by the flame photometry method (Jeddi and Chaieb, 2010).

c. Calcium and Magnesium concentrations were determined using atomic absorption spectrophotometry (Jeddi and Chaieb, 2010).

d. The percentage of sand, clay and silt were determined using a hydrometer.

e. Electrical Conductivity was analysed electrometrically using a digital bench-top multi-range (H18820) conductivity meter.

f. Total nitrogen was determined by the use of Kjeldahl procedure ((Jeddi and Chaieb, 2010).

g. Phosphorus was determined using the Bray No.11 method (Jeddi and Chaieb, 2010).

h. Organic carbon was determined using the Walkley-Black method (Jeddi and Chaieb, 2010).

4.4.3 Data Analysis

Differences in soil nutrient concentrations and forage consumption with distance from the stock posts (100, 500 and 1000 m) and between plains and foothills were analyzed using two-factor ANOVA. Three Way ANOVA was used to test for differences in biomass production, species richness and diversity with distance from the stock posts, between plains and foothills, between years (2006 versus 2007) and vegetation types. Plant species diversity in in each of the sample plots in the five vegetation types was calculated using the Shannon – Wiener Diversity Index (H') using the formula (Diversity Index (H') = -∑ Pi In Pi, where Pi = ni/N is the number of individuals found in the ith species as a proportion of total number of individuals (n) found in all species (N), while In is the natural logarithm to base e.) as described by Brown *et al*., (2016).

Species richness was calculated using the Simpson Index as the number of species represented in each sample plot and transect. It is simply a count of species found in a specific area (Brown *et al*., 2016) which in this case in each sample plot, transect and vegetation type. The relationships between rainfall and biomass production, species richness and diversity were determined by use of linear regression. All analyses were performed using STATISTICA software version 8 and SAS software version 9.

In order to determine the influence of environmental variables on plant species composition and distribution, ordination was done using Canonical Correspondence Analysis (CCA) on vegetation data using the ECOM II software package (Hejcmanová-Nežerková and Hejeman, 2006). The environmental variables were first tested for multi-collinearity after which variables with close correlations were excluded from the CCA analysis. Variables that were excluded after multi-collinearity test include Sodium, Potassium and Carbon. Environmental variables that were included in CCA analysis comprised of rainfall, distance from stock posts, soil pH, phosphorus, magnesium, EC, nitrogen and calcium. Species abundance data (dry mass per m^2) were not transformed (because they did not vary much) unlike the environmental and soil variables which were square-root transformed due to huge variance of measurements. Very rare species (those that appeared only once) in all sample plots were excluded from the ordination analysis.

4.5 Results

4.5.1 Rainfall data

The monthly rainfall data that was recorded at each of the five rain gauges in the five study sites in RNP for the two years of study were obtained from the South African Weather Service in Pretoria. The 5 rain gauges belongs to the Park, and the RNP staff usually record rainfall data in each rain gauge and submit the data to South African Weather Service. Figure 4.4 shows the annual rainfall that was recorded in RNP in each of the 5 vegetation types in 2006 and 2007 when the vegetation and soil sampling was done. Vegetation types Northern Richtersveld Scorpionstailveld (NRS) and Central Richtersveld Mountain (CRM) found in the western and central part of the park in the Succulent Karoo Biome recorded the highest amount of rainfall in 2006 and in 2007 compared to the vegetation types found in the Desert biome. Vegetation types Northern Richtersveld Scorpionstailveld (NRS), Richtersveld Sheet Wash Desert (RWSD), Richterberg Mountain Desert (RMD) and Noms Mountain Desert (NMD) in the Desert Biome in RNP recorded lower amount rainfall in 2006 and 2007. In 2006 rainfall recorded in RNP was relatively high ranging between 78 mm in the Desert biome and 248 mm in the Succulent Karoo biome, while in 2007 the amount of rainfall that was recorded was above average ranging between 54 mm in the desert biome and 176 mm in the Succulent Karoo as shown in Figure 4.3.

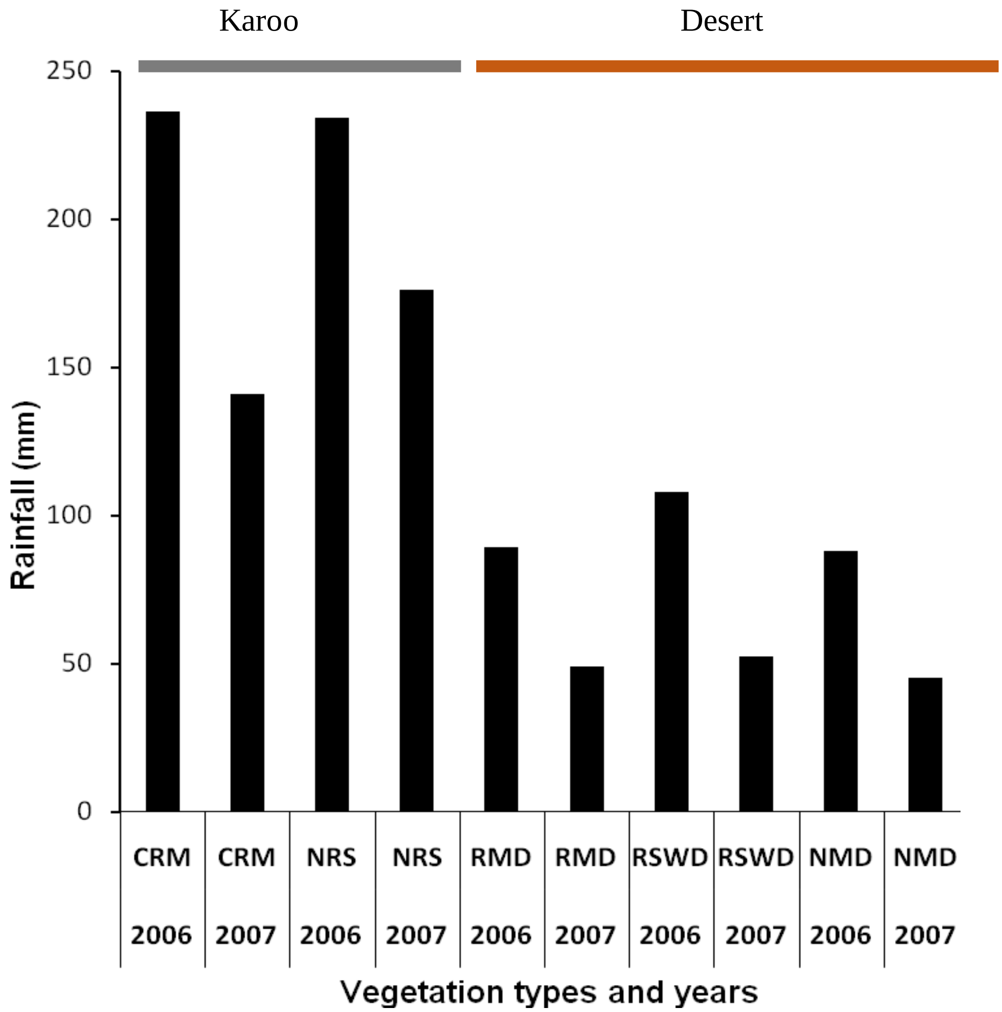


Figure 4.3: Rainfall data recorded in the 5 vegetation types found in RNP in 2006 and 2007

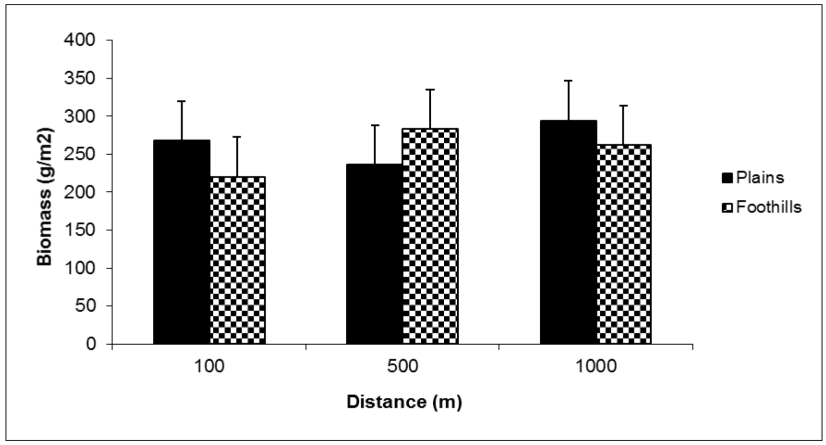
4.5.2 Effects of rainfall, landforms and grazing on annual plants on biomass production, species richness and diversity.

Biomass production did not differ significantly between the two landscapes (P = 0.06) and with distance from the stock posts (P=< 0.05) but differed significantly with rainfall (P< 0.05) (Figure 4.4a-c, Table 4.1). Biomass production and species diversity were significantly higher on the plains than on foothill. Species diversity differed significantly between the two landscapes and with distance from the stock posts, but did not differ with rainfall. Species richness differed significantly with distance from the stock posts and with rainfall, but did not differ between the two landscapes (Table 4.1).

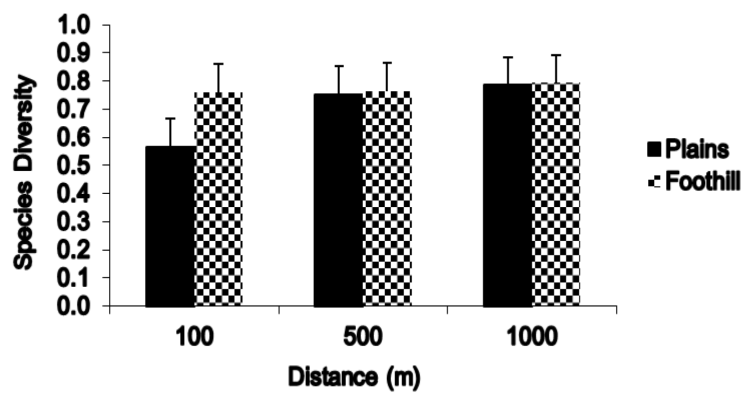
Table 4.1: ANOVA results of the effect of distance from the stock

Plant parameters	Distance	Landforms	Rainfall
Biomass production	$F_{(2,57)} = 3.12$ P>0.05 289± 6	$F_{(1,58)} = 0.52$ P>0.05 302 ± 8	$F_{(1,58)} = 36.90$ **P< 0.05** 316±11
Species richness	$F_{(2,57)} = 3.12$ **P< 0.05** 0.8± 0.2	$F_{(1,58)} = 0.04$ P>0.05 0.7±0.1	$F_{(1,58)} = 41.65$ **P< 0.05** 0.8±0.2
Species Diversity	$F_{(2,57)} = 6.74$ **P< 0.05** 0.7± 0.2	$F_{(1,58)} = 4.77$ **P< 0.05** 0.7±0.2	$F_{(1,58)} = 0.11$ P>0.05 0.8±0.1

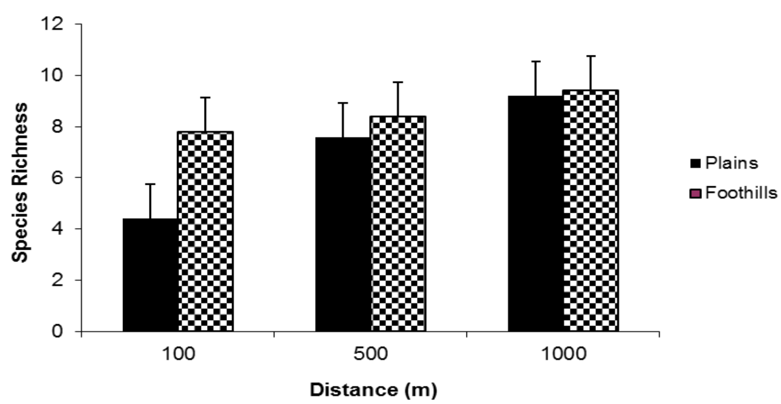
Biomass production did not differ significantly with distances from the stock posts as shown in Figure 4.4a. Species richness differed significantly with distances from stock posts only at 100 m from the stock posts, but did not differ both on the plains and foothills at 500 and 1000 m from stock posts (Figure 4.4c). Species diversity increased with increase with distances away from the stock posts on the plains, but did not differ significantly on the foot hills landscapes (Figure 4.4b)



(a)



(b)



(c)

Figure 4.4a-c: Effect of grazing (distance from stock posts) on biomass production, species diversity and richness of annual plants

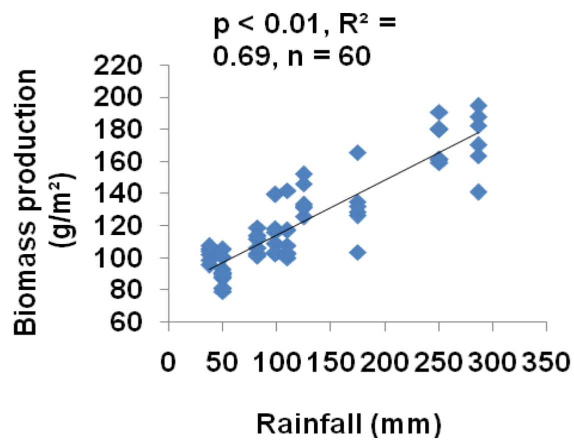
C. Biomass production in different vegetation types

There was a significant difference in biomass production between the vegetation types ($P<0.05$, $N = 60$). Biomass production was significantly higher in vegetation types NRS and CRM than in vegetation types NMD, RMD and RSWD. Species richness and diversity were also significantly higher in Succulent Karoo vegetation than in desert biome vegetation types as shown in Table 4.1, (vegetation type NMD received both winter and summer rainfall). Biomass and species richness from the NMD vegetation type was intermediate between the two biomes. Biomass production, species richness and diversity did not differ significantly between vegetation type CRM and NRS in Succulent Karoo biome and also did not differ significantly between vegetation types NMD, RMD and RSWD which are in the desert biome (Table 4.1).

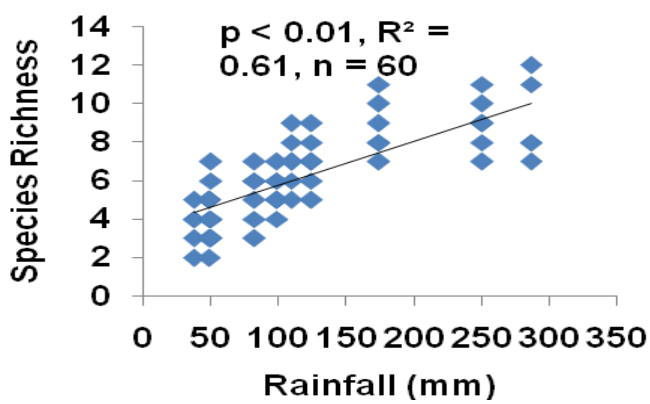
4.5.3 The relationship between rainfall and biomass production, species richness and species diversity

Biomass production, species richness and diversity were positively correlated with rainfall as shown in Figure 4.5a-c. Biomass had a strong correlation with rainfall with $R^2 = 0.69$, species richness with $R^2 = 0.60$ while species diversity had correlation of $R^2 = 0.61$.

(a)



(b)



(c)

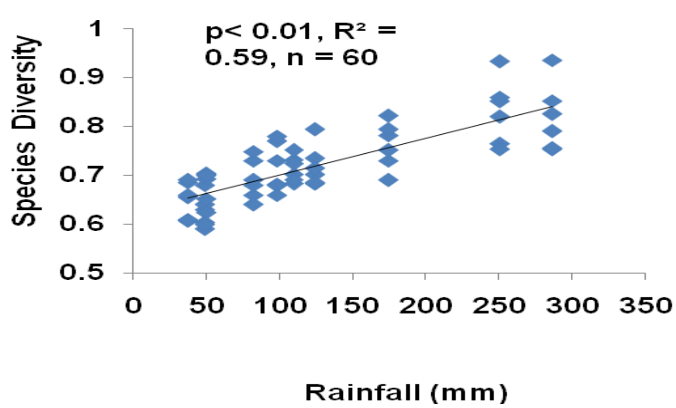


Figure 4.5a-c: Relationship between biomass, species richness and diversity with rainfall.

Biomass production was significantly higher in 2006 than in 2007 ($F_{(1, 58)} = 36.90$, $P < 0.01$, n=60, Figure 4.6c). Species richness was higher in 2006 than in 2007 (Figure 4.1a) while species diversity did not show significant differences between the years (Figure 4.6b). Biomass production, species richness and diversity were also significantly ($P<0.05$) greater in vegetation types CRM and NRS found in the Succulent Karoo Biome than in vegetation types RMD, RSWD and NMD found in desert biome (Figure 4.6a-c). This may be attributed to differences in the amount of rainfall between the two years and between the vegetation types. Different letters denote significant difference while similar letters show no significant different.

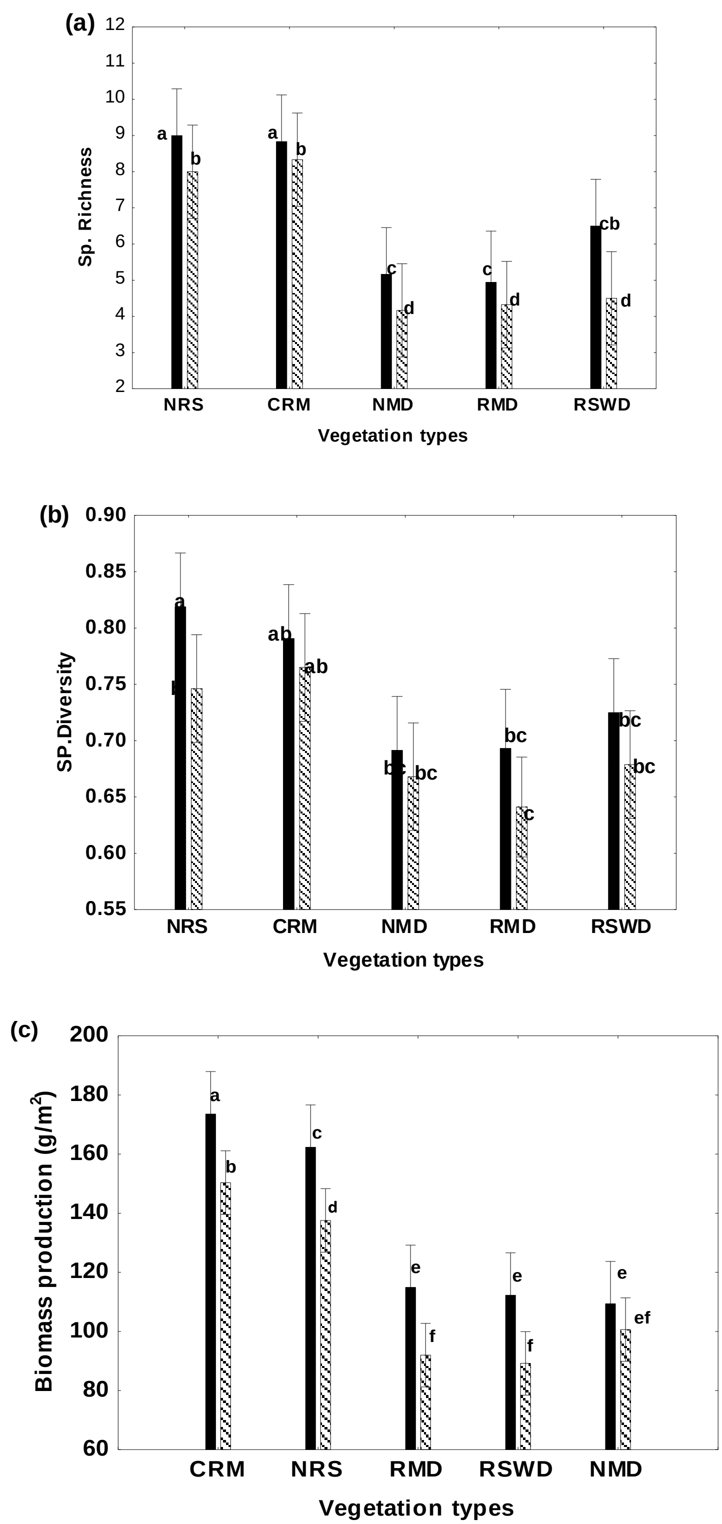


Figure 4.6a-c: Biomass, species richness and diversity in 5 vegetation types.
(2006 2007 Vertical bars denote 0.95 confidence intervals).

4.5.4 Variation of soil properties with grazing and in landscapes

Most of soil nutrients (Calcium, Magnesium, potassium, phosphorous, and sodium) decreased significantly with distances away from stock posts (Table 4.2). Mg, P, Na, N, soil pH differed significantly with distance from the stock posts as shown by the highlighted figures in table 4.2 with $P < 0.05$. There were significant differences in the concentration of phosphorous, pH, sodium and nitrogen between the plains and the foothills while the rest did not show significant difference between the two land forms (Table 4.2).

Table 4.2: Variation of concentration of soil variables along grazing gradient and land forms

The highlighted values in bold show significant difference at $P < 0.05$.

Soil Nutrients	**Distance**	**Land forms**	**Distance x Land forms**
Calcium	$P > 0.05$; $F_{(2, 23)}=5.34$	$P >0.05$; $F_{(1, 23)}=1.6$	$P >0.05$; $F_{(2, 23)}=0.24$
Magnesium	**$P< 0.05$**; $F_{(2, 23)} = 4.58$	$P >0.05$; $F_{(1, 23)} = 0.04$	$P >0.05$; $F_{(2, 23)}= 0.43$
Phosphorus	**$P< 0.05$**; $F_{(2, 23)} =5.90$	**$P<0.05$**; $F_{(1,23)} = 6.84$	$P >0.05$; $F_{(2, 23)}=1.79$
Sodium	**$P< 0.05$**; $F_{(2, 23)}=2.78$	$P>0.05$; $F_{(1, 23)} = 0.039$	$P>0.05$; $F_{(2, 23)}=0.03$
Nitrogen	**$P< 0.05$**; $F_{(2, 23)}=3.30$	**$P<0.05$**; $F_{(1, 23)}=6.93$	$P >0.05$; $F_{(2, 23)}=0.56$
Soil pH	**$P<0.05$**; $F_{(2, 23)}=4.58$	**$P<0.05$**; $F_{(1, 23)}=9.51$	$P >0.05$; $F_{(2, 23)}=1.92$
Carbon	$P > 0.05$; $F_{(2, 23)}=1.8$	$P >0.05$; $F_{(1, 23)}=2.28$	$P >0.05$; $F_{(2, 23)}=.094$
EC	$P >0.05$; $F_{(2, 23)} =1.96$	$P >0.05$; $F_{(1, 23)}=3.01$	$P >0.05$; $F_{(2, 23)}=0.78$

(Units of measurements of soil parameters: pH – KCl, Phosphorus (Bay II – mg/kg, Exchangeable cations - Na, Mg, Ca, K- Cmol(+)/kg; Carbon - %; EC-Mɥ)

Nitrogen, sodium and phosphorus were significantly higher on the plains than on the foothills while calcium, EC and soil pH were higher on the foothills than on the plains (Table 4.3). Most of the soil nutrients were significantly higher in CRM and NRS vegetation types in succulent biome than in NMD, RMD and RSWD vegetation types in desert biome). Soil PH, sodium and potassium were significantly higher in NMD, RMD and RSWD vegetation types (Table 4.3). The ANOVA results in table 4.3 show that most soil variables differed significantly at $p<0.05$ between the vegetation types except for Mg, pH and EC. The results also indicate that all soil variables differed significantly with distances from the stock post except Electrical Conductivity (EC). Most soil variables also differed significantly at $p<0.05$ between the landforms except for Mg, K and EC.

Table 4.3: Means of soil parameters with distance from the stock posts, with vegetation types and landforms

Data points labeled with the same letter are not significantly different. (Units of measurements of soil parameters: pH – KCl, Phosphorus (Bay II – mg/kg, Exchangeable cations - Na, Mg, Ca, K- Cmol(+)/kg; Carbon - %; EC - Mų); (mean±se)

	Ca	Mg	K	P	pH	Na	N	C	EC
Distance:									
100m	1.18±0.4a	13.6±3.2a	2.4±0.9a	19.2±5.8a	7.8±3.9a	13.5±2.2a	2.3±1.4a	0.06±0.3a	0.25±0.2a
500m	0.88±0.3b	8.6±2.6b	1.16±0.7b	8.0± 4.6b	7.4±3.1b	9.3±2.7b	1.5±0.7b	0.05±0.03b	0.16±0.13b
1000m	0.53±0.2b	6.1±3.0c	0.69±0.3c	4.4±2.9c	7.0±2.8c	5.9±1.8c	1.3±0.5b	0.04±0.02b	0.11±0.06c
LSD P<0.05)	0.26	4.7	1.01	8.67	0.56	2.36	0.69	0.006	0.14
Veg. types:									
CRM	1.16±0.9a	10.4±4.3ab	1.4±0.4b	17.1±6.5a	7.0±3.1b	8.4±4.4c	2.4±1.4a	0.07±0.02a	0.19±0.07b
NRS	1.12±0.8a	9.2a±6.5b	0.7±0.3b	16.7±10ab	7.1±2.3b	5.7±3.6c	2.3±1.7a	0.07±0.03a	0.1±0.05c
NMD	0.62±0.4b	13.9±5.3a	3.4±2.0a	10.7±8.8b	7.5±3.3a	16.4±4.2a	1.6±0.5b	0.04+0.01b	0.3±0.01a
RMD	0.65±0.3b	7.4±2.6b	0.9±0.3b	2.3±1.2b	7.9±2.7a	11.7±5.1b	0.6±0.2c	0.03+0.01c	0.16±0.1ab
RSWD	0.78±0.5b	6.6+2.9b	0.5±0.2b	5.8±3.4c	7.6±1.9a	5.8±3.8c	1.3±0.4c	0.04+0.02b	0.12±a0.1b
LSD P<0.05)	0.33	6.09	1.31	11.2	0.73	3.05	0.89	0.01	0.19
Landforms:									
Plains	0.76±0.4a	9.7±2.8a	1.48±0.5a	15.3a	7.0±3.8a	10.8±4.2a	2.2±1.3a	0.06±0.03a	0.13±0.07a
Foothills	0.97±0.5b	9.2±3.0a	1.36±0.8a	5.7b	7.7±4.0b	8.3±3.7a	1.2±0.6b	0.04±0.02a	0.23±0.05b
LSD P<0.05**)**	0.21	3.9	0.83	7.07	0.46	1.92	0.56	0.005	0.12

4.5.5 Effect of rainfall, grazing and soil variables on species composition and distribution

Ordination was used in this study to order the arrangement of plant species in relation to each other in terms of the similarities of species composition and their associated environmental control variables. From the ordination diagrams (Figures 4.7 and 4.8) arrows pointing in the same direction indicate a high correlation while arrows crossing at right angles indicate near zero correlation and arrows pointing in roughly opposite direction indicate a high negative correlation. In the two vegetation biomes, it was found that rainfall had the greater influence on plant species composition than grazing (distance from the stock posts) and soil properties. In desert biome, the soil properties that had the greatest influence on plant species, included magnesium, phosphorous, EC and calcium (Figure 4.7). In the Succulent Karoo biome, soil pH, calcium, nitrogen and phosphorous had the greatest influence on distribution of plant species (Figure 4.8). Result shows that the effect of grazing that was represented by distances from stock post had less effect on composition of annual plants than rainfall.

In the desert biome, distribution of plant species *Heliophila trifurca* (Brassicaceae), *Hypertelis salsoloides (*Aizoaceae*), Nemesia strumosa* (Scrophulariaceae)*, Oncosiphon grandiflorum (*Asteraceae*)* and *Dimorphotheca sinuate (*Asteraceae*)* were mainly influenced by calcium and nitrogen concentration in the soil while *Dimorphotheca tragus (*Asteraceae*), Ornithoglossum viride (*Colchicaceae*), Cotula barbata (*Asteraceae*), Tribulus cristatus (*Zygophyllaceae*), Acanthopsis disperma (*Acanthaceae*)* and *Wahlenbergia sp. (*Campanulaceae*)* were highly influenced by rainfall. On the other hand *Mesembryanthemum nodiflorum (Aizoaceae), Amellus nanus (Asteraceae), Stoeberia beetzii var beetzi (*Aizoaceae*), Schmitdtia kalahariensis (Poaceae)* and *Oncosiphon suffruticosum (Asteraceae)* were influenced by grazing (distances from stock posts) as shown in Figure 4.7.

In succulent Karoo biome, the distribution of plant species *Gorteria personata (*Asteraceae*), S. beetzii var beetzii (*Aizoaceae*), and Nemesia anisocarpa (*Scrophulariaceae*)* were highly influenced by Mg and Ca while *Hirpicium echinus (*Asteraceae*), Pentizia incana (*Asteraceae*), Stoeberia beetzi (*Aizoaceae*)* were influenced by grazing (distance from the stock posts). Plant species *Amellus nanus (*Asteraceae*), Trianthema sp.(*Aizoaceae*), Oncosiphon grandiflorum (*Asteraceae*), Dimorphotheca sinuate (*Asteraceae*), Mesembryanthemum guerichianum (*Aizoaceae*)* and *Cotula barbata (*Asteraceae*)* were closely associated with presence of phosphorus and nitrogen in soil while *Vigna vexillata var. ovate (*Fabaceae*), Oncosiphon suffruticosum (*Asteraceae*), Schmitdtia kalahariensis (*Poaceae*), Heliophila trifurca (*Brassicaceae*)* and *Limeum* africanum *L. subsp. Africanum* (Molluginaceae) were highly influenced by rainfall (Figure 4.8)

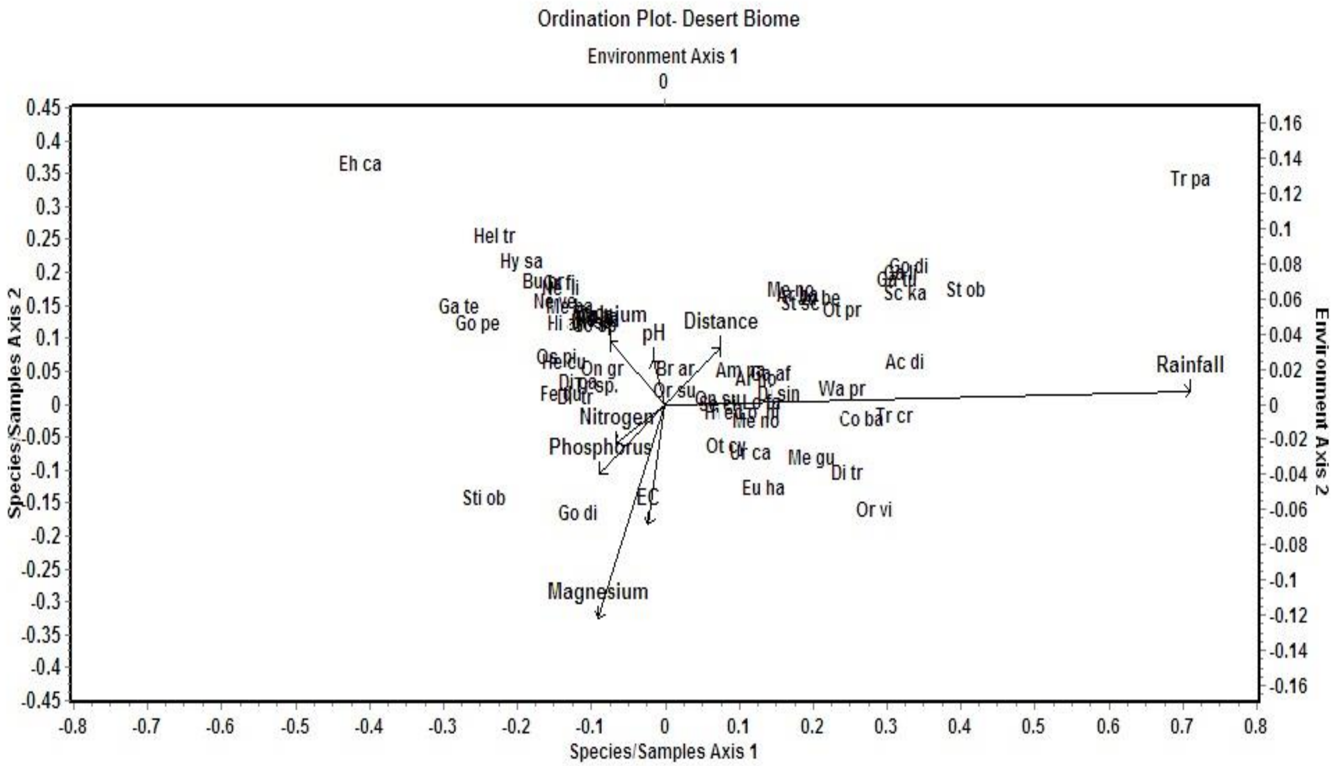


Figure 4.7: Biplot Ordination scatter diagram showing influence of environmental variables on distribution of plant species in Desert Biome in RNP

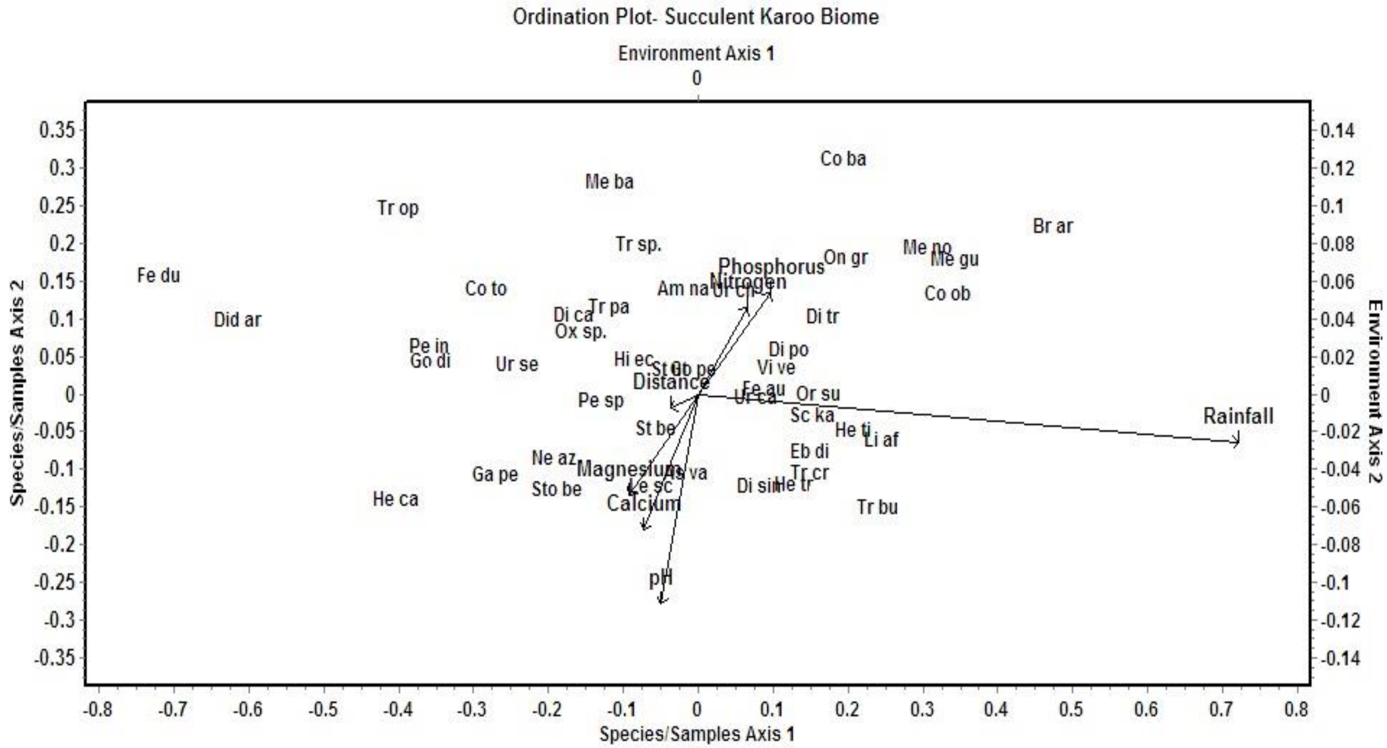


Figure 4.8: Biplot Ordination scatter diagram showing influence of environmental variables on distribution of plant species in Succulent Karoo Biome in RNP

Arrows represents environmental variable and abbreviated letters represents plant species listed below. Abbreviated species were: – He tr -*Heliophila trifurca*, Hy sa - *Hypertelis salsoloides*, Ne st - *Nemesia strumosa*, On gr -*Oncosiphon grandiflorum*, Di si -*Dimorphotheca sinuate*, Di tr -*Dimorphotheca tragus*, Or vi -*Ornithoglossum viride*, Co ba - *Cotula barbata*, Tr cr - *Tribulus cristatus*, Ac di - *Acanthopsis disperma*, Am na -*Amellus nanus*, St be -*Stoeberia beetzii var beetzi*, Sc ka -*Schmitdtia kalahariensis*, On su -*Oncosiphon suffruticosum* belonging to various plant families as shown in Table 4.4

Arrows represents environmental variables and abbreviated letters represents plant species listed below. Abbreviated species names were Go pe - *Gorteria personata, S. beetzii var beetzii*, Ne an -*Nemesia anisocarpa*, Hi ec -*Hirpicium echinus*, Pe in -*Pentizia incana*, St be -*Stoeberia beetzi*, Am na -*Amellus nanus*, Tr sp. -*Trianthema* sp, On gr -*Oncosiphon grandiflorum*, Di si -*Dimorphotheca sinuate*, Co ba - *Cotula barbata*, Vi ve -*Vigna vexillata var. ovate*, On su -*Oncosiphon suffruticosum*, Sc ka -*Schmitdtia kalahariensis*, He tr -*Heliophila trifurca*, Li af -*Limeum africanum L. subsp. Africanum*, He tr -*Heliophila trifurca*, Hy sa -*Hypertelis salsoloides*, Ne st -*Nemesia strumosa*, On gr -*Oncosiphon grandiflorum*, Di si - *Dimorphotheca sinuate*, Di tr -*Dimorphotheca tragus*, Or vi -*Ornithoglossum viride*, Co ba - *Cotula barbata*, Tr cr -*Tribulus cristatus*, Ac di -*Acanthopsis disperma*, Wa pr -*Wahlenbergia sp.*, Am na -*Amellus nanus*, St be -*Stoeberia beetzii var beetzi*, Sc ka -

Schmitdtia kalahariensis, On su - *Oncosiphon suffruticosum* belonging to various families as shown in Table 4.4.

Table 4.4: Annual plant families found in RNP

	Plant Families	No. of Plant Species	% Frequency	Growth Forms
1	Asteraceae	43	35.8	Herbs
2	Aizoaceae	23	19.2	Leaf succulent/ herbs
3	Scrophulariaceae	11	9.2	Herbs
4	Poaceae	8	6.7	Grass
5	Fabaceae	5	4.2	Herbs
6	Acanthaceae	3	2.5	Herbs
7	Asphodelaceae	3	2.5	Leaf-Succulents
8	Zygophyllaceae	3	2.5	Herbs/ shrubs
9	Boraginaceae	2	1.7	Herbs
10	Brassicaceae	2	1.7	Herbs
11	Colchicaceae	2	1.7	Herbs
12	Crassulaceae	2	1.7	Leaf-Succulents
13	Asparagaceae	1	0.8	Herbs
14	Caesalpiniaceae	1	0.8	Herbs/shrubs
15	Campanulaceae	1	0.8	Herbs
16	Capparaceae	1	0.8	Herbs / lianas
17	Euphorbiaceae	1	0.8	Leaf/stem succulents
18	Hyacinthaceae	1	0.8	Herbs/ bulbs
19	Iridaceae	1	0.8	Herbs
20	Limeaceae	1	0.8	Herbs/ shrubs
21	Molluginaceae	1	0.8	Herbs
22	Santalaceae	1	0.8	Herbs/shrubs
23	Solanaceae	1	0.8	Herbs, shrus/lianas
24	Tecophilaeaceae	1	0.8	Herbs, geophytes/ climbers
25	Urticaceae	1	0.8	Herbs/ lianas

The number of plant species that were encountered during the winter season were 120 species (as shown in appendix 1), and they belonged to 25 different plant families (Table 4.4). In terms of frequency of occurrence, the plant family Asteraceae had the highest (35.8 %), followed by Aizoaceae (19.2 %), Scrophulariaceae (9.2 %) and Poaceae (6.7 %). The other 21 plant families had less than 5% frequency of occurrence as shown in Table 4.4.

4.6 Discussion

4.6.1 Effect of rainfall on biomass production, species richness and diversity of annual plants in RNP

Results from this study indicated that rainfall strongly influenced biomass production of annual plants in all vegetation types, and this can be attributed to the higher rainfall that was recorded in 2006 than in 2007. Vegetation types in the Succulent Karoo biome in the western side of RNP received high winter rainfall and therefore recorded higher biomass production, species richness and diversity than the desert biome in the northern and southern part of the study area with more scattered summer rainfall and very little winter rainfall leading to an overall more erratic rainfall pattern, sometimes of less than 80 mm per year. High primary productivity has been associated with high rainfall (Anderson *et al.*, 2011). Species composition and diversity of annual plants were significantly altered by rainfall.

The study shows annual plants are more productive in good rainfall years and are an important component of the winter diet. For example, in a study that was done in the same study area in a very dry period in 1998 and 1999 (Hendricks *et al*. (2005b), very few annual plants species (only 9 species of annual plants) were recorded in RNP by) compared to the reported mass growth of annual plants (128 species) that were recorded in 2006 and 2007 when this study was conducted. This shows that contribution of annual plants to forage is very variable and dependent primarily on rainfall in addition to their large and diverse seed bank (van Rooyen *et al*, 2018). Annual plants therefore play an important role as substitute source of forage for herbivores in rangelands especially immediately after a dry period as they germinate faster.

4.6.2 Effect of landforms and distances from stock posts on soil variables

The observed increase in soil pH, phosphorus, magnesium, sodium, and potassium near the stock posts (designated places where animals congregate in the evening) can be attributed to the high concentration of herbivores dung and urine around the stock posts. This study found low organic carbon, nitrogen, calcium and electrical conductivity in the study area and higher phosphorus, magnesium and sodium. Effects of large quantities of animal dung and urine within the vicinity of stock posts and watering points on the increase of P, Na, Mg and K contents in the soil was also observed. Most of soil nutrients in this study differed significantly at a distance of 100 m from the stock posts as change in soil properties and most of the nutrients generally occurred within 100 m from the stock posts.

There was low level of nitrogen content in RNP in Succulent Karoo. This can be attributed to the fact that nitrogen can be lost due to denitrification faster than other elements such as phosphorous that do not have atmospheric phase in their cycles. Also plants utilize nutrients available in the soil for their growth and they deplete nutrients from the soil during the growth period considering that the study was conducted during wet seasons when there was mass growth of annual plants. It was also noted in this study that in the composition of annual plants encountered, there were few species of legume family that are known to fix nitrogen. This may have contributed to low nitrogen levels in the soil.

Increased soil nutrients accumulation near the stock posts was attributed to presence of animal dung and urine near the stock posts as herbivores aggregate every evening. These were clear evidence of the existence of piosphere effect (effect of dung and urine) on concentration of soil nutrients around the stock posts in RNP.

4.6.3 Effect of landforms and grazing on biomass production, species richness and diversity of annual plants in RNP

Plant species diversity was found to be higher on the plains than on foothills at a distance of 100m in 2006 while there were no differences in species richness and biomass production between the two landforms. High species richness and diversity is a characteristic feature of the succulent Karoo biome as reported by Mucina and Rutherfold, (2006) and Anderson and Hoffman (2011). Anderson and Hoffman (2010) found higher perennial species diversity on the rocky foothills than on the sandy plains in a communally grazed land in Succulent Karoo as well as more vegetation cover loss on the plains than on the foothills.

Therefore, in higher rainfall years, the open spaces created by loss of larger plants due to grazing effects especially on flat plains are usually colonized by geophytes and annual plants species and this leads to high growth of annual plants in Succulent Karoo during the wet seasons (Anderson and Hoffman, 2007). Therefore, variation of forage production and intensity of grazing in different landscapes were observed in this study, meaning spatial heterogeneity of resources was evident in RNP.

4.6.4 Influence of environmental variables and grazing on plant species composition and distribution

The environmental variables influenced the distribution of different species in RNP as each plant species has specific habitat conditions, ecological needs and tolerance range. From the ordination diagrams, species composition and distribution were different in succulent and desert biomes. This shows that the two biomes exhibit different environmental and edaphic variables. The soil characteristics that were found to influence plant species composition included magnesium, phosphorus, EC, pH and calcium (Figure 4.7 and 4.8). The CCA output showed that rainfall had greater influence on species composition in RNP than grazing (distances from stock posts) and soil nutrients in both biomes. On the other hand, distance from the stock posts had very minimal influence on species composition both in Succulent Karoo and in Desert Biome.

This study showed how rainfall variability in Succulent Karoo affects annual plant species leading to variability in forage quality and quantity in arid areas. In the light of the ongoing climate change, the predicted decrease in rainfall and rise in temperatures in succulent karoo (MacKellar *et al.,* 2007) will consequently affect biomass production in the vast winter rainfall areas of RNP. If climate change effects (such as low winter rainfall, erratic rainfall patterns, prolonged droughts and very high temperatures) occur as per the predictions of Young *et al.,* (2016) in Succulent Karoo, then loss of succulent plants in winter rainfall area such as RNP will have negative impact on primary productivity, livestock farming and on the livelihoods of communities that rely on pastoralism as well as the entire biodiversity of the Succulent Karoo biome.

The issue that needs to be addressed is whether these ecosystems, such as RNP are ecologically resilient enough to withstand the effects of climate change scenario (present in the Succulent Karoo) in addition to the unsustainable land use practices, such as continuous communal grazing by pastoralists who rely on these arid ecosystems.

4.6.5 Conclusions on drivers and dynamics of annual vegetation in RNP

This study clearly shows that in RNP climatic factors play a substantial role in influencing vegetation growth more than grazing. Rainfall had greater impact on primary productivity, species richness, diversity and distribution of annual plants species than grazing which is a characteristic of a non-equilibrium dynamics during the rainy season. Rainfall variability which is common in Succulent Karoo affects the productivity, diversity and composition of annual plants leading to spatial-temporal resource heterogeneity. The study shows that annual plants were less influenced by grazing compared to rainfall. This shows that in RNP during wet season, there is enough forage supply by annual plants to support herbivores populations in a density-independent manner.

The establishment of watering points and stock posts in the rangelands has been found to alter the spread and occurrence of plants species and soil nutrients thus would recommend the need to review establishment of additional stock posts in the RNP to reduce the observed piosphere effects.

Deposition of animal pellets and urine around the stock post has affected the distribution of soil nutrients most of which decreased with increase in distance from the stock posts. Establishment of more stock posts in the area will only escalate this problem by spreading the piosphere effects to the other parts of the landforms.

This implies that in case of an occurrence of a prolonged dry period there is likelihood of animal loss due to lack of forage. Therefore, study of factors that drives forage production, composition and distribution as well as determining the existence of equilibrium and disequilibrium dynamics in RNP offers an opportunity to understand the environmental processes in this dry ecosystems.

CHAPTER 5: TEMPORAL AND SPATIAL HETEROGENEITY OF FORAGE PRODUCTION BY SHRUBS IN RNP

5.1 Introduction

This chapter examines how forage production by perennial shrubs varies with time in different landscapes and vegetation types in RNP. The purpose of this chapter is to estimate spatial and temporal variation in biomass production by shrubs across the RNP in three landscapes (flat plains, foothills and mountains). The study also seek to find out whether remote sensing data and amount of rainfall can be used to estimate and predict forage production in arid rangelands as well as in identification of forage hotspots for the herbivores.

5.2 Spatial-temporal heterogeneity of forage production by shrubs

Forage production and distribution in arid rangelands is not uniform but varies with seasons in various landscapes (Easdale and Aguiar, 2012). Pastoralists take advantage of spatial heterogeneity as rainfall and forage resources are not uniformly distributed in the rangelands. Spatial heterogeneity also helps to buffer effects of climatic variability in rangelands since herbivores can utilize forage in different landscapes at different seasons (Samuels *et al.*, 2013). Such movement of animals between landscapes may be transhumance whereby pastoralists follow predictable patterns between rainy and dry seasons, or movements may be opportunistic following unpredictable patchy rainfall patterns (Vetter, 2005; Samuels *et al.*, 2013). Temporal and spatial heterogeneity of resource distribution in rangelands, coupled with herbivore movement patterns, enables pastoralists to maintain high stocking rates without putting continuous grazing pressure on the environment (Salomon *et al.*, 2013).

Arid rangelands are not only inconstant in their production of fodder for livestock production, they are also very volatile systems (Eisfelder *et al.*, 2014). Therefore, for effective utilization of forage in these ecosystems by herbivores as well as formulation of proper management policies there is need to understand spatial and temporal forage production and factors that influence forage productivity in rangelands (Rasch *et al.*, 2016).

Information on spatial and temporal forage production and variability is crucial to pastoralists, rangeland managers and policy makers in making decisions on issues related to conservation and management of rangeland ecosystems (Jakoby *et al.*, 2015). The forage production capacity of any rangeland has been found to be the principal variable that limits stocking rates (Notenbaert *et al.*, 2012). Risks associated with over-grazing occur mainly due to lack of detailed information on temporal and spatial variation in primary productivity in rangelands.

In RNP there are distinct wet season resources (annual plants and shrubs found on the plains and mountains) that animals utilize during the winter rain seasons between the month of May to September and dry season resources (trees and grasses along the Orange River riparian zone) where herbivores migrate to during the dry season that mostly occurs between October and April every year. An understanding of spatial forage variability in forage production would help the pastoralists in RNP to manage their livestock, determine the stocking rates in a sustainable manner.

This component of the study aimed to investigate how forage production by shrubs varies in space and time in RNP. The aims were to:

(i) Determine the temporal and spatial variation in biomass production by shrubs in different vegetation types and landscapes.

(ii) Calibrate remote sensing values of fPar for pixels that corresponded to the ground sampling in location and date and using this calibration, use remote sensing imagery from 2002-2007 to estimate spatial and temporal variation in biomass production across the RNP.

(iii) Determine the influence of rainfall and grazing on in biomass production by shrubs in different vegetation types and landscapes

5.3 Materials and Methods

5.3.1 To assess spatial and temporal variation in biomass production in different landscapes, and vegetation types

Transects to measure perennial biomass production were laid at the study site in each of the five vegetation types (Figure 3.2) on three landscapes (flat plain, foothills and on the mountains). At each study site, three transects were laid one on each landscape i.e. on the flat plains, foothills and on the mountains, amounting to 45 (1 km^2) plots sampled (15 plots per landscape and per transect). A total of 225 plots were sampled in the 5 study sites (3 landscapes per site, 15 plots per landscape and 45 plots per site for 5 sites). Three transects at each landscape position, totalling to nine transects per study site and 45 in total for the 5 study sites. In each of the 1 km^2 plots, 20 lines (20 m long) were laid at a distance of 10 m apart parallel to each other. The line intercept method was used to determine the percent canopy cover of perennial shrubs. This was done by recording the horizontal distances covered by live crown along the 20 m line (Flombaun and Sala, 2007). The length of the line intercept of plant species along the 20 m lines were recorded.

In addition to measuring the twenty, 20 m lines in each 1 km^2 plots, ten $20m^2$ plots were measured and within the $20m^2$ plots, 5 sub-plots of $5m^2$ were measured (Figure 5.1). Inside the $5m^2$ plots, two parallel lines were laid at 20cm from the edge of the plot and all the intercepted plants (shrubs) within the 5m² were harvested after measuring their canopy intercept along the 2 parallel lines (Flombaun and Sala, 2007).

All the current season's green biomass (twigs and leaves) of the intercepted plants were harvested and separated into the three main plant growth forms (stem succulents, leaf succulents, and non-succulents). The harvested plant material was oven-dried in the laboratory at 70° C for 48 hours and weighed. The regression equations that were obtained between the measured length of the intercepted canopy cover and dry mass of the harvested plants were used to estimate the biomass production of the 1 km^2 plot based on the canopy cover estimated by the line intercept method (Flombaun and Sala, 2007).

5.3.2 Estimation of biomass production using remote sensing data

To quantify primary productivity using remote sensing technique, pre-processed Moderate Resolution Imaging Spectroradiometer (MODIS) imageries were downloaded from Land Processes Distributed Data Archive (Land Process DAAC National Center, EROS Sioux Falls, SD, USA) for the period corresponding to the dates (from 26th June to 2nd August 2007) when the ground measurements of biomass production were collected. Fraction of photosynthetic active radiation (fpar) values from MODIS imageries which consisted of 8 days composite images at spatial resolution of 1 km² pixel size were extracted.

The fraction of photosynthetic active radiation (fpar) values were extracted from the pixels that matched the ground co-ordinates and dates when the ground measurements of biomass production were collected. MODIS imageries were downloaded and fraction of photosynthetic active radiation (fpar) values extracted for the selected pixels in all the vegetation types for the period from 26th June to 2nd August 2007 corresponding the dates when the ground measurements of biomass production were collected. In addition MODIS imageries were downloaded for the year 2002 to 2007 and fpar values were extracted. It was not possible to obtain fpar values in the vegetation type Richtersveld Sheet Wash Desert (RSWD) because the area is largely covered by sand on the plains and rocks on the foothills and mountains and therefore vegetation type RSWD was excluded from the analysis.

5.3.3 Rainfall data

Rainfall data were recorded in 5 rain gauges in the 5 vegetation types (each vegetation type had a rain gauge).

5.4 Data analysis

To determine the relationships between canopy cover and above ground biomass production for different growth forms linear regression analyses was performed with biomass production as dependent variable and line intercept cover as the independent variable. General Linear Model (GLM) was used to compare variation in biomass production in amongst the three growth forms found in the four vegetation types. The relationship between above ground dry biomass and remote sensing data (fpar) was determined using linear regression analyses. GLM was also used to determine the variation of above ground biomass in the 3 landscapes (plains, foothills and mountains) with biomass as dependent variable and vegetation types and landscape as categorical variables.

General Linear Model was used to determine intra and inter- annual variations in primary productivity in the 4 vegetation types. The correlations between rainfall with biomass production and fpar values was determined by use of linear regressions with winter period rainfall as independent variable while biomass production and fpar values were considered as the dependent variables. The regression equation that was obtained was used to convert the fpar values obtained from MODIS for the 6 years (2002-2007) to biomass production in kg/Ha.

5.5. Results

5.5.1 Rainfall in RNP

Vegetation types Northern Richtersveld Scorpionstailveld (NRS) and Central Richtersveld Mountain (CRM) found in the western and central part in the succulent karoo biome recorded the highest amount of rainfall between 2002 and 2007. Vegetation types Northern Richtersveld Scorpionstailveld (NRS), - Richtersveld Sheet Wash Desert, RMD- Richterberg Mountain Desert

(RSWD) and Noms Mountain Desert (NMD) in the Desert Biome in RNP recorded lower amount rainfall in the 6 years period. The highest amount of rainfall was also recorded in 2006 and 2007. Recorded rainfall was lowest in 2004 as shown in Figure 5.1.

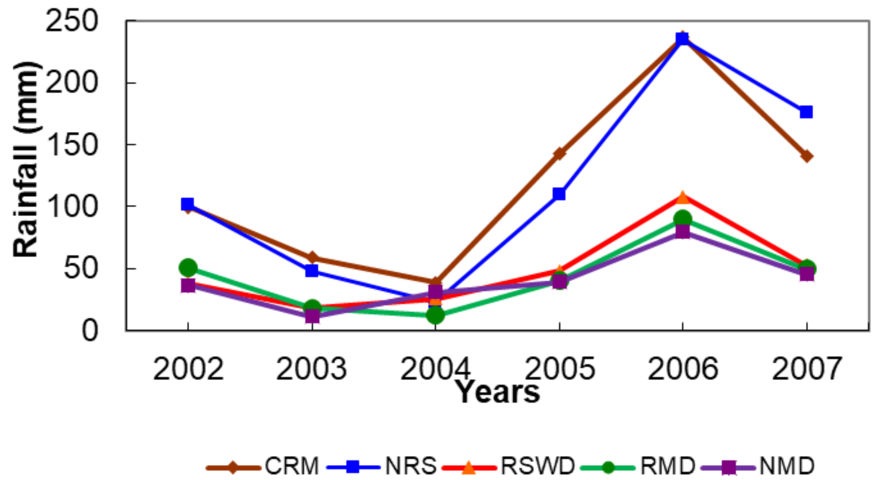


Figure 5.1: Annual rainfall data for the 5 vegetation types

Vegetation types represented in Figure 5.1 were: CRM - Central Richtersveld Mountain, NRS - Northern Richtersveld Scorpionstailveld, RSWD - Richtersveld Sheet Wash Desert, RMD - Richterberg Mountain Desert and NMD - Noms Mountain Desert

5.5.2 Spatial and temporal variation in biomass production in different vegetation types and landscapes

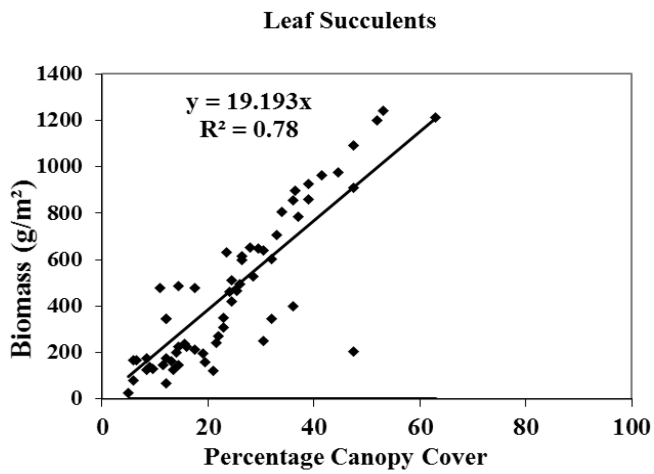
The regression equations obtained between above ground biomass production and percentage canopy cover were positive for the three growth forms (leaf succulents, stem succulents and non-succulents) as shown in Figure 5.2a-c. Leave succulents had the highest coefficient of determination ($R^2 = 0.78$, $P<0.05$), non-succulents had R^2 of 0.72 and $P < 0.05$ while stem-succulents had the lowest coefficient of determination ($R^2 = 0.67$, $P< 0.05$) as shown in Figure 5.2a-c and table 5.1 below. The regression equations between the harvested above ground biomass and the percentage canopy cover in each plant category (stem-succulents, leaf-succulents and non-succulents) were later used to convert the measured intercept vegetation cover to biomass production.

Biomass production by stem and leaf succulents plants were significantly different in the succulent Karoo biome in vegetation types CRM and NRS ($P < 0.05$) but did not differ significantly in vegetation types NMD, RMD and RSWD in the desert biome (Table 5.1). Biomass production by non-succulents did not differ significantly ($P>0.05$) in all vegetation types in both succulent and desert biomes. Total biomass was significantly higher in vegetation types CRM and NRS in succulent Karoo biome than vegetation types in desert biome as shown in Table 5.1. In Table 5.1 shown below, the figures with different letters within the same column are significantly different while figures with similar letters within the same column are not significantly different (P value < 0.05); Mean biomass in g/m^2.

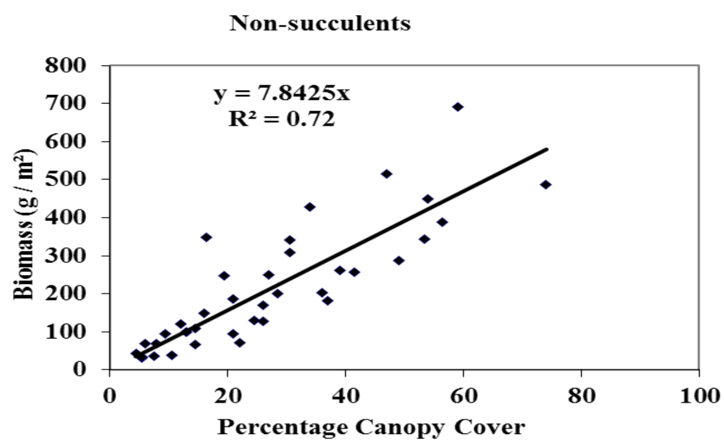
Table 5.1: Variation in biomass production in different vegetation types and landscapes

Biomes	Veg. types	Mean Biomass (g/m^2) by plant types			
		StemSuccul	Leaf Succul	Non-Succ	Total Biomass
Succulent Karoo	CRM	726.32[a]	350.90b	63.36a	962.8a
	NRS	317.81[b]	560.28a	20.46a	934.7a
Desert Biome	NMD	84.80cd	65.05c	12.37a	209.5b
	RMD	27.60d	22.40c	7.51a	98.5b
	RSWD	21.42d	26.19c	5.73a	81.6b

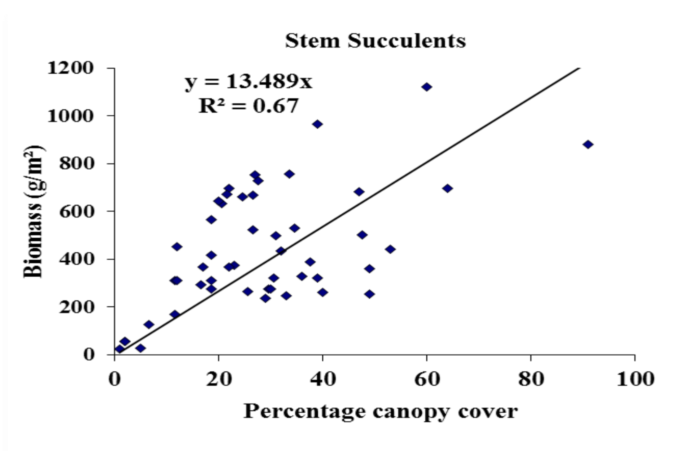
Biomass production was higher in Northern Richtersveld Scorpionstailveld (NRS) and Central Richtersveld Mountain (CRM) vegetation types found in the western and central part of the park in the Succulent Karoo Biome (Figure 5.3) The two vegetation types also recorded the highest amount of rainfall during the 2 years of study (in 2006 and 2007). The other three vegetation types (Richtersveld Sheet Wash Desert, Richterberg Mountain Desert, and Noms Mountain Desert) found in Desert Biome had low forage production compared to the Succulent Biome. In CRM vegetation type biomass production was higher on the flat plains than in foothills and mountain landscapes. In contrast, NRS vegetation type had higher biomass production was higher on the foothills and mountains landscapes than on the flat plains.



(a)



b)



c)

Figure 5.2a-c: Percentage canopy cover and biomass production for different growth forms

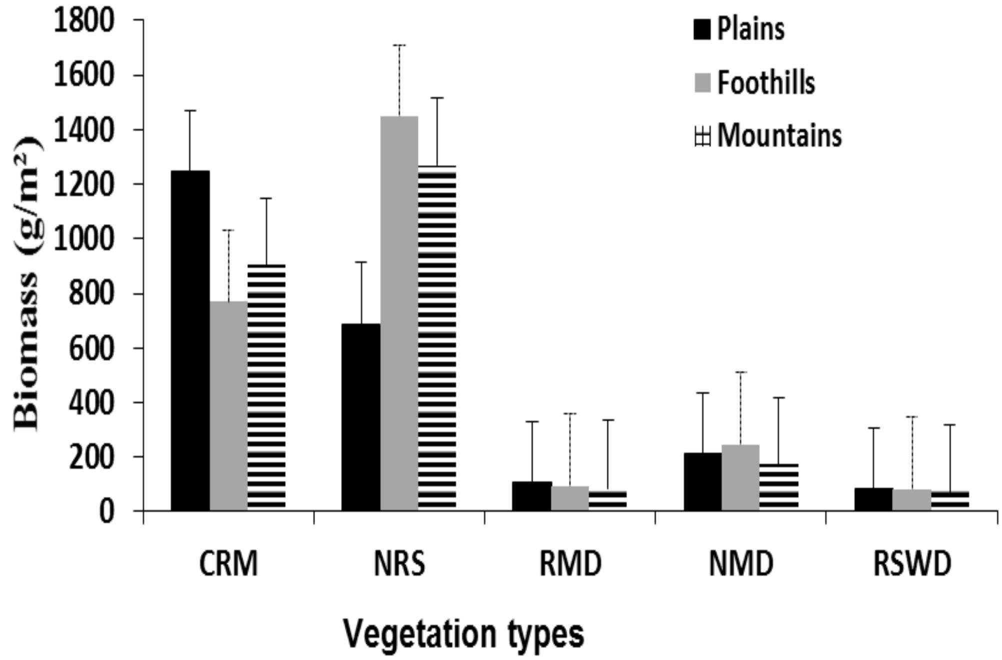


Figure 5.3: Variation in biomass production in different landscapes

Vegetation types - CRM-Central Richtersveld Mountain, NRS- Northern Richtersveld Scorpionstailveld, RSWD- Richtersveld Sheet Wash Desert, RMD- Richterberg Mountain Desert, NMD- Noms Mountain Desert

5.5.3 Relationship between above ground biomass production and fpar

There was a strong relationship between above ground biomass production and fpar values (R^2 = 0.89) as shown in Figure 5.4. The relationship was linear because in arid areas, immediately after the onset of rains, and there is moisture in the soil, germination, sprouting and vegetation growth takes place very fast and this leads to increased rate of photosynthesis and the observation fraction of photosynthetic active radiation (fpar) values. With time the linear (curvilinear) curve will level off and stabilize at the point when the vegetation growth reaches the maximum due to limitation of other ecological factors such as competition for resources.

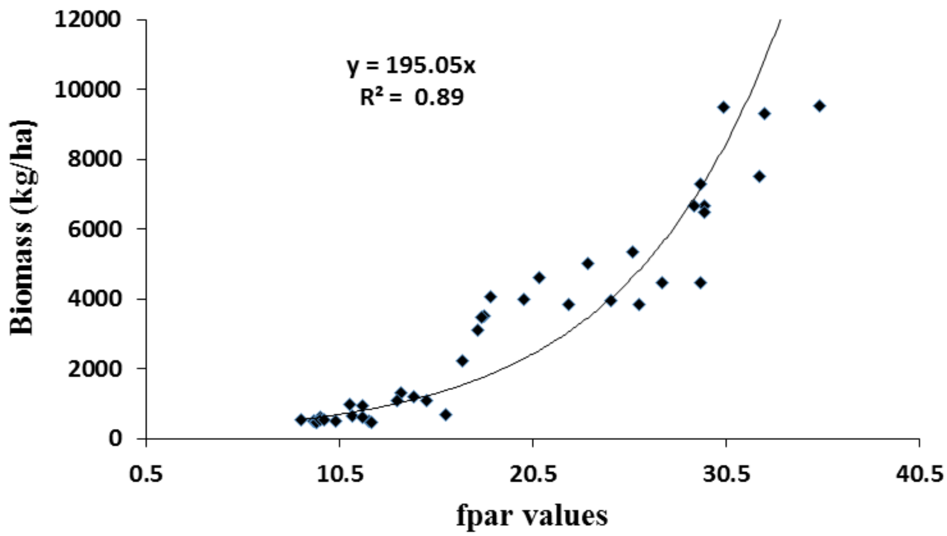


Figure 5.4: Relationship between above ground biomass production and fpar

The vegetation types from the Desert Biome (RMD and NMD) recorded low biomass production as shown in in Figure 5.5. Peak fpar values were recorded during the winter months (June to September) while August was the month with the highest fpar values in all vegetation types for the 6 years (Figure 5.5).

The Succulent Karoo biome had higher fpar values than the desert biome throughout the years in all vegetation types. It was not possible to obtain fpar values in most parts of the vegetation type Richtersveld Sheet Wash Desert (RSWD) because the area is largely covered by sand on the plains and rocks on the foothills and mountains and therefore fraction of photosynthetic active radiation could not be obtained (recorded zero).

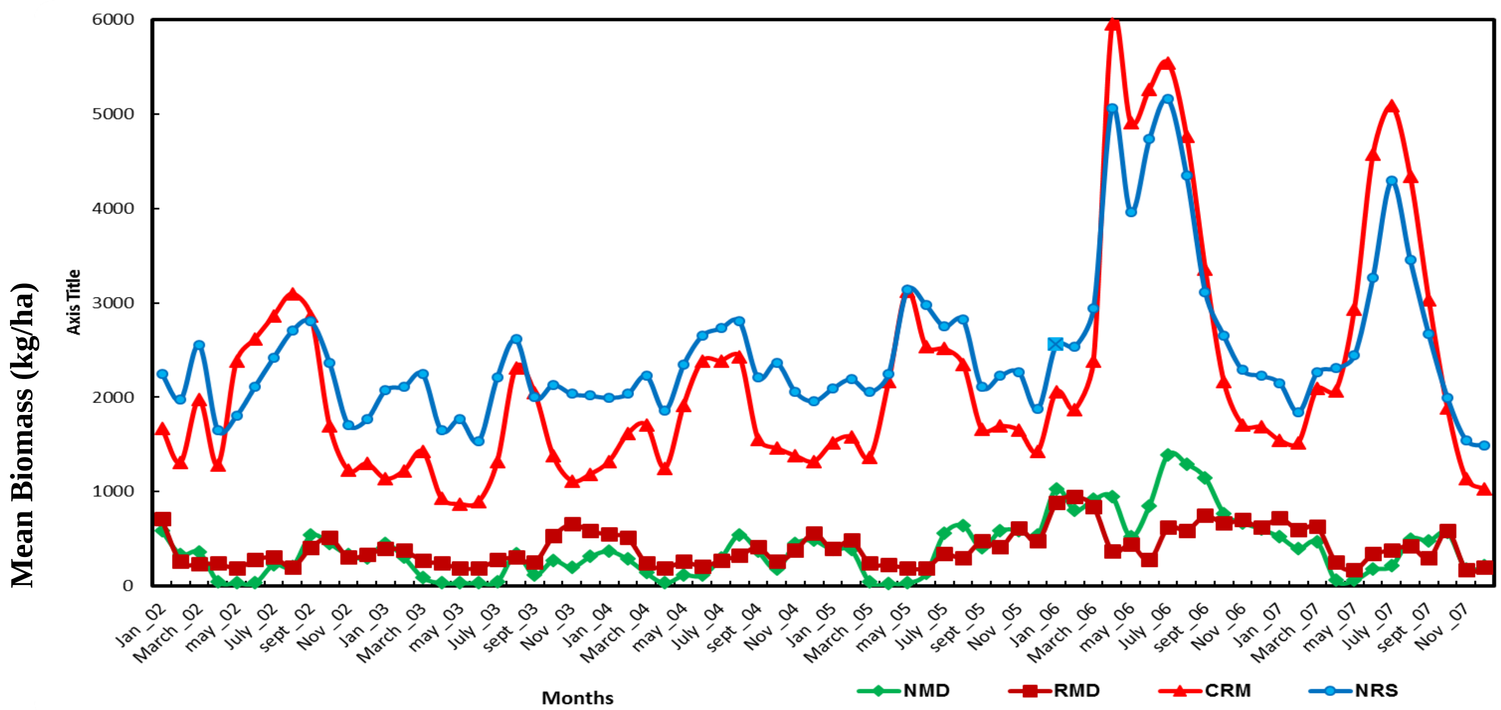


Figure 5.5: Spatial-temporal variation in biomass production in the 4 vegetation types in NRP.

Symbols of distinct are- ●NRS- Northern Richtersveld Scorpionstailveld, ▲CRM-Central Richtersveld Mountain, ■ RMD- Richterberg Mountain Desert and ♦NMD- Noms Mountain Desert.

5.5.4 Influence of rainfall on biomass production by perennials

There was a strong linear relationship between amount of rainfall received and above ground biomass production ($R^2 = 0.73$, $y = 16.391x - 302$ and $P < 0.01$). There was also a strong correlation between the amount of rainfall and fpar values obtained ($P<0.01$, $R^2 = 0.79$, $y = 12.794x - 307.18$). Both fpar values and above ground biomass production increased with increase in rainfall in this arid ecosystem (Figure 5.6 and Figure 5.7).

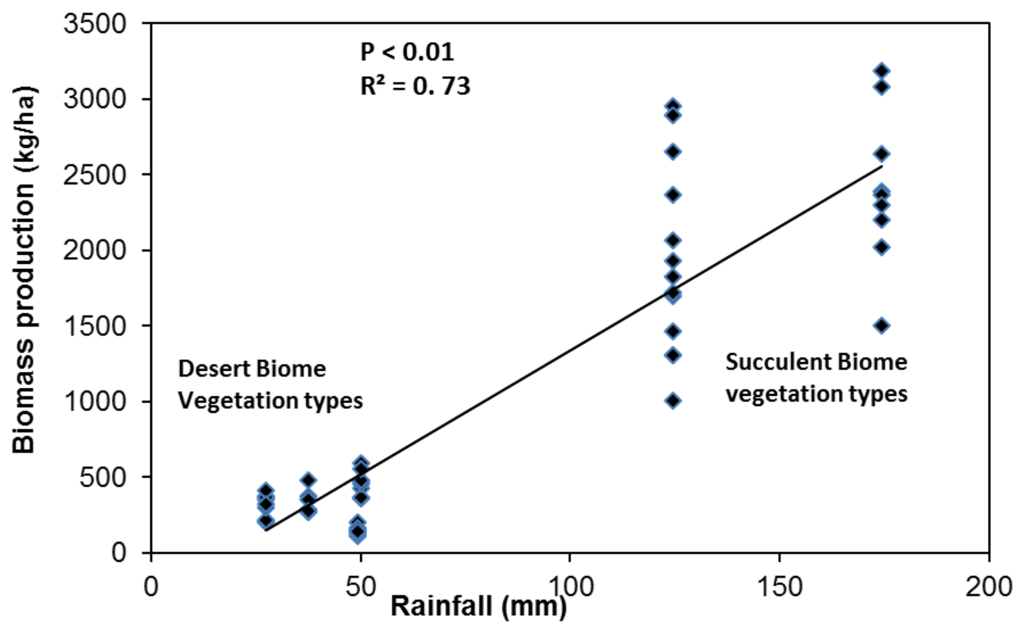


Figure 5.6: Relationship between above ground biomass production and rainfall in 2007 for the 5 rain gauges in the 5 vegetation type's in RNP.

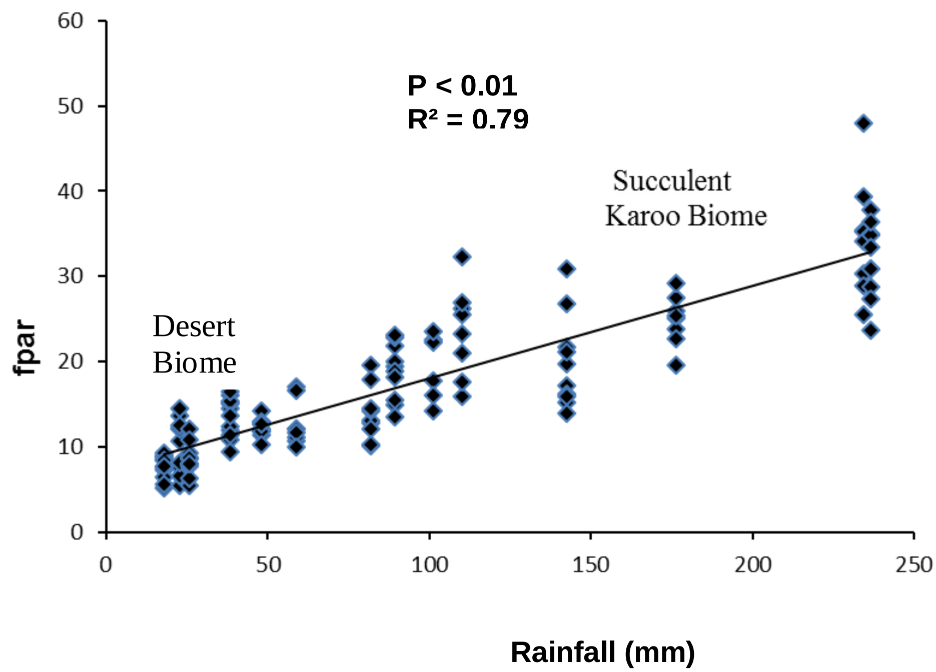


Figure 5.7: Relationship between fpar values (of plots where harvesting of biomass took place) and rainfall.

5.6 Discussion

5.6.1 Spatial and temporal variations in forage production

The variability in biomass production in different landscapes and vegetation types reflected heterogeneity of plant growth as a result of variations in climatic and ecological attributes in the study area. The study showed that biomass production varied between the vegetation types and in different landscapes. Biomass production was found to be higher in vegetation types located in the succulent Karoo biome which may be attributed to higher winter rainfall that was recorded in Succulent Karoo biome than in the Desert Biome. On the other hand vegetation types in the desert biome produced less forage because they also received less amount of rainfall. This clearly show that biomass production of perennial plants in arid ecosystems, such as RNP are highly influenced by rainfall. Leaf succulents contributed the highest amount of forage, followed by stem succulents while non-succulents contributed the least amount of forage. Not all forage available in RNP was utilized by the herbivores, as animals were found to graze more on the flat plains and foothills and less in the mountains (personal observation). The mountainous landscapes in RNP are steep and rocky, and herbivores were found not to graze on the mountains. There was also no stock posts on the mountainous landscapes as most stock posts were found on the plains.

In RNP herbivores utilized different landscapes at different seasons in a year. They were found to settle on the plains and foothill landscape during the wet season and along the Orange River riparian zone during the dry season. Therefore, the study of temporal, seasonal and spatial variations in biomass production and distribution in RNP is of great importance to land users as it will enable them to know when and where forage is existing at different seasons in a year. Alternating landscape and seasonal resource use impose a cycle of plant growth and phenology resulting into forage availability at different seasons. Spatial separation of landscapes accessible during the wet and dry seasons is therefore regarded as having significant effect on the dynamics of herbivores and their effect on vegetation. Spatial variability of forage resources buffer seasonal variability of animal populations by providing a refuge resource to herbivores during the drought (Jakoby *et al.,* 2015).

The observed change of biomass production with seasonality concurred with Anderson and Hoffman (2010) and Palmer and Yunusa, (2011) who also found that the intra-annual relationships between biomass production and Normalized Difference Vegetation Index (NDVI) changed with seasonality. Plant growth in the Succulent Karoo occurred in winter period when there was precipitation and most of herbaceous plants died off after spring except for the perennial succulent shrubs that were adapted to withstand the high temperatures in summer and this may have been the cause of low primary productivity recorded during the dry period in the area (Hempson *et al.*, 2015).

Fog from the Atlantic Ocean is another source of moisture on the western side of RNP (Succulent Karoo Biome) and plays a great role in sustaining vegetation growth (Mucina *et al.,* 2006). The arid rangelands, such as RNP, are usually characterised by low and erratic rainfall which in turn leads to unpredictable forage production within and among years (Rutherfold and Powrie, 2010). Due to high rainfall variability, the primary productivity fluctuates widely whereby high forage production is witnessed in years of high rainfall and low productivity in dry years. Droughts are a common occurrence in this rangelands (Hendricks *et al.,* 2005b) that cause deaths of herbivores thus reducing their populations. Recovery of herbivore populations depended on forage availability which only occured after rains (Hendricks *et al.,* 2005b; Hempson *et al.,* 2015). This may be interpreted to mean that precipitation regulates forage productivity in RNP. Strong relationships between rainfall and biomass production showed that rainfall was one of the significant factor that influenced primary productivity in rangelands which consecutively regulated the herbivores populations in this ecosystem as reported by Hempson *et al.,* (2015).

Remote Sensing data and line-intercept method were found to be suitable tools in measurement of heterogeneity in forage productivity in RNP. This was attributed to the strong relationships obtained between remote sensing fpar values with biomass production as well as with rainfall. In addition, MODIS data are widely available in finer spectral resolutions and in combination with in-situ (harvested) biomass data confirmed that they can be used in regular valuation of spatial-temporal variation in fodder productivity in heterogeneous rangelands such as RNP as well as in identification of forage hotspot areas for the herbivores (Ngugi and Conant, 2008; Jakoby *et al.*, 2015).

Remote sensing fpar values can be effective in monitoring and predicting spatial and temporal variation in biomass production in this arid ecosystem because measure of fraction of photosynthetic active radiation is interpreted as a reflection of the amount of biomass productivity of the vegetation in an area. Remote sensing data (fpar values) are also very useful in estimating and extrapolating biomass production for a long period over time. It was therefore possible to estimate and extrapolate biomass production over a period of 6 years (2002-2007) in the 4 main vegetation types in RNP using fpar values.

Strong relationships between biomass and vegetation productivity index NDVI and MODIS have been reported in rangelands (Palmer and Yunusa, 2011; Rutherfold and Powrie, 2011; Hempson *et al.,* 2015). However, the relationship between fpar values and biomass was stronger than with rainfall. This could be attributed to the application of larger and variable remote sensing data compared to few points of rainfall data collected in a small number of rain gauges in the study areas (Tsalyuk *et al.,* 2015). Fpar values are frequently and widely available even during the dry periods and are more suitable in predicting temporal primary productivity than the rainfall data that are only available during the rainy seasons. Also Satellite imageries, such as MODIS are good predictor of forage productivity because fpar is sensitive to the photosynthetic processes of plant canopies at a finer temporal and spatial resolution.

However, despite the wide applicability and accuracy of Remote sensing data in measurement of biomass production, this technology has some disadvantages. Lack of technical know-how on how to access or use remote sensing data has hindered many from utilizing it (Eisfelder *et al.,* 2014). Secondly, remote sensing data is not applicable in a small finer scale because only a single unit data can only be extracted in a pixel of $1km^2$ (Gillan *et al.,* 2019). Another shortcoming of use of remote sensing data in assessing primary production is that the technology can only capture photosynthetic active radiation (fpar values) only in areas with vegetation cover. Areas that are largely covered by water, sand and rocks the fraction of photosynthetic active radiation cannot be obtained (Palmer *et al*., 2015). Remote sensing data (fpar) can over-estimates the available forage because it captures photosynthetic radiation of all vegetation, including forage that is not accessible by herbivores, for example in the top canopies and inaccessible areas (Gillan *et al*., 2019).

Information on temporal and spatial variations in primary productivity with rainfall patterns will therefore contribute to the understanding of the effects of climate change on plant communities in this arid area, which is predicted will be one of the most severely affected (Young *et al.,* 2016). The study showed that leaf and stem succulents' plants contributed the highest amount of available forage production in most parts of this dry ecosystem and therefore such landscapes should be given conservation priority.

5.6.2 Implications of spatial-temporal heterogeneity to rangeland management

The management policies in arid rangelands, such as RNP should embrace the observed equilibrium and non-equilibrium dynamics that arise due to spatial and temporal heterogeneity in forage production, in order to cushion pastoralists from the effects of climatic variability and for effective plants conservation. Proper understanding of temporal and spatial variability in primary productivity in African rangelands has ecological as well as economic implications. In livestock farming, information on rangeland productivity would help pastoralists to make informed decision in tracking the availability of forage resources for their herbivores as well as act as a guide in decision making on the maximum number of animals which would provide maximum yields (Fynn, 2012). This study has shown that the forage productivity of this dry ecosystem is variable in space and time and therefore flexible movement to track forage would be very critical due to existence of less anticipated patterns of forage production caused by irregular rainfall patterns.

Forage tracking strategies based on distribution of primary productivity are environmentally friendly and wastes less feed (Jakoby *et al.,* 2015). According to Jakoby *et al.,* 2015, high spatial and temporal heterogeneity in resources within an ecosystem buffer the risks associated with productivity shortages as a result of climatic fluctuations. Pastoralists in RNP use animal mobility and landscape partitioning as a response to spatial-temporal heterogeneity in order to manage livestock and ecosystem resources effectively. Herbivores were found to graze first on the forage-rich flat plains, followed by foothills and eventually move to hilly areas towards the end of the wet season. Not all forage available in RNP was utilized by herbivores especially on the mountainous landscapes due to inaccessibility. Further there was need of animals to drinking water and high temperatures that force herbivores to migrate to the key resource areas (along the river belt zone) on the onset of the drought (Hendricks *et al.,* 2005b). This also supports the view that during the rainy season in RNP there is imbalance between the available forage resources and herbivores numbers as depletion of resources rarely occur in such a disequilibrium dynamic.

Herbivore mobility has been regarded to be advantageous in livestock production as well as in biodiversity conservation (Samuels *et al.,* 2013; 2019). When pastoralists understand and utilize heterogeneity in forage production in relation to variable climatic factors, this reduces their vulnerability to the effects of unpredictable climatic factors that have been observed to greatly influence forage production.

5.6.3 Conclusion and recommendations

The study showed that:

(i) Use of remote sensing data, such as MODIS imageries, collected at high frequency, made it possible to track productivity changes and habitat quality at a smaller scale in RNP with possibilities of going back in time and covering a large area within a short period of time. This technique was useful in this study in measurement of primary productivity in areas of the park that were difficult to access such as the mountains and steep valleys.

(ii) The study has demonstrated that remote sensing data and rainfall patterns can be used to estimate and predict forage production in rangelands as well as in identification of forage hotspots for the herbivores.

(iii) Information on variation of forage production from this study will be useful in rangeland management and in regulation of land use practices such as pastoralists' nomadic movement patterns as well as resource utilization by herbivores.

(iv) Since pastoralists graze their animals in the park, and they move from one place to another tracking forage, information on variation in biomass production in arid ecosystem will act as a guide to the park managers on the maximum carrying capacity as well as to the nomadic pastoralists on forage hotspot areas in different seasonality.

From this study the following recommendations were made:

(i) The park managers to advocate for herbivores mobility so that pastoralists can utilize forage resource heterogeneity found in different landscapes at different seasons. Herd mobility would reduce the vulnerability of pastoralism to the effects of unpredictable climatic conditions that have been observed to greatly influence forage production and availability.

(ii) Modelling of forage production with remote sensing (fpar) and rainfall data would be recommended in order to predict long term effect of rainfall on forage production.

(iii) Regular monitoring of vegetation biomass production using remote sensing technology, such as MODIS should be conducted so that the information can assist pastoralists in identification of forage hotspots in different landscapes and seasons.

CHAPTER 6: SPATIAL-TEMPORAL VARIATION IN FORAGE PRODUCTION ALONG THE ORANGE RIVER RIPARIAN BELT IN RNP

6.1 Introduction

This chapter investigates the spatial-temporal variation in forage production and utilization along the Orange River riparian zone (a key dry season resource), how the available browse forage from trees and grasses vary with time and the contribution of this key resource area in the pastoral systems in RNP.

6.2 Forage production along the riparian zone as a dry season resource

Studies have shown that pastoralists have adjusted to alternative livestock management approaches that guide them to manoeuvre in arid ecosystems that are characterised by unstable climatic conditions and diverse resource variability (Salomon *et al.,* 2013). Other studies have shown that the number of herbivores that survive during the drought in rangelands are largely dependent on their ability to exploit parts of the landscapes that are rich in resources.

These key resource areas include riparian zones, drainage lines as well as high quality forage, fruits and flowers associated with trees. The grazing pressure in the landscape as a whole therefore becomes dependent on the relative amount of key resource. Thus during the growing (rainy) seasons when the key resources is not being utilized, animals disperse through the landscape perhaps giving the impression of little coupling between animals and vegetation by reducing the grazing pressure (Vetter, 2005).

In arid rangelands, such as RNP, the riparian zones act as a grazing reserve or fall-back area during the dry periods. Due to harsh climatic conditions in these ecosystems, availability of herbaceous plants is limited by rainfall (Saayman *et al.*, 2018) while differences in the phenology cycles of browse species make it possible for forage to be available at different times of the year (Naah and Guuroh, 2017). Legume plants, such as *Acacia karoo* and *Prosopis glandulosa* have been introduced in dry areas to solve the problems of feed deficiency, as most of native pastures are of low quality, quantity and poor digestibility during the dry seasons (Ganqa and Scogings, 2007), although in RNP they grow naturally (not introduced species).

Legume trees and shrubs have been found to be rich in proteins, minerals and vitamins and are available throughout the year even in areas with harsh climatic conditions (Olafadehan and Okunade, 2018). In the management of rangelands, there is need to understand the diet preference of herbivores as this influences when and where the animal spends their time browsing. The quality and quantity of available browse forage, time spent browsing and the influence of the pastoralists collectively determines the productivity of animals in the rangelands (Salomon *et al.*, 2013).

In RNP, the dry season forage consists mainly of tree branches, leaves, flowers, bark, bulbs, tubers, seed pods and fruits (Hendricks *et al.*, 2005b). In addition there is fallen litter from the upper canopy of trees as well as grass that grows along the Orange River. In many studies, litter is usually an overlooked forage source on browse estimates despite the fact that it contributes significantly to the diet of ruminants (Muller *et al.*, 2012).

According to van der Vyver and Cowling (2019) litter as foliage falling from top canopy is more palatable due to low concentration of secondary metabolites in higher browse than lower growing foliage and also has greater nutritional quality than hard wood browse. Skarpe *et al.,* (2007) found that goats preferred browse from higher branches compared to the lower ones. Litter fall occurs in most part of the year and therefore contributes considerably to the total forage especially when there is browse shortage.

Browse production fluctuates between and within years depending on the type of plant species (Leparmarai *et al* 2018). For example, evergreen species have browse production throughout the year while that of deciduous trees are seasonal. Not all forage produced by trees and shrubs is available to animals due to height effect (Baumert and Khamzina, 2015); for example in RNP, goats could only utilize browse from trees up to a height of 1.5 meters (Hempson *et al.*, 2015). Other factors found to deter full browse utilization include presence of secondary metabolites, high fibre content and morphological traits such as thorns and spines

(Leparmarai *et al.*, 2018). Some proportion of browse is unpalatable and this has led to an over-estimation of available forage (Gillan *et al.*, 2019) which could be the case in RNP and in other rangelands.

Measurement of browse production is regarded as a difficult, tedious, time-consuming and costly activity (Skarpe *et al.*, 2007). Methods of measuring browse production that have been used include visual estimates and harvesting (Ganqa and Scogings, 2007), use of regression equations between trees biomass and their dimensions (Gillan *et al.*, 2019) and use of allometric models (Baumert and Khamzina, 2015). Visual estimation methods are considered inexpensive and faster but are hindered by observer's personal judgement, lack of verifiable levels of statistical confidence and precision (Tolleson *et al.*, 2019).

On the other hand, harvesting methods are expensive, tedious and time consuming and therefore a combination of the two methods has been recommended to calibrate the more time- and cost-effective visual estimation methods (Tolleson *et al.*, 2019). The regression equations between trees biomass and their dimensions (mostly of branches weight-diameter relationship) have been widely used and strong correlations between the two parameters with biomass production have been reported (Baumert and Khamzina, 2015).

Browse production along a riparian zone may be influenced by several ecological factors, such as rainfall and river water levels. It is important to note that forage production in the riparian zone are not synchronised with those of the wet season resource, because the wet season resource responds so strongly to rainfall but the main water source of the riparian zone was the Orange River. The river water levels are mainly determined by rainfall in the summer rainfall regions in the interior of South Africa.

Orange River is one of the longest river in South Africa (Williamson, 2000a). The river forms the boundary of South Africa and Namibia in Richtersveld area. It is a perennial river whose water flows from far beyond RNP. Being a perennial river, it plays an important ecological role in supporting the growth of the riverine vegetation throughout the year. The river water levels in RNP varies with seasons and thus influences availability as well as accessibility of forage to herbivores (personal observation). When the river water levels are high, grass forage is usually covered by water due to floods and therefore becomes inaccessible to goats. On the other hand, when the river water levels are low, the grass becomes accessible to goats. The river water levels were not dependent only on rainfall that was recorded in RNP but the river water flows from the entire catchment areas all the way from Lesotho, Botswana and Namibia (Williamson, 2000a). So it was prudent in this study to find out whether browse production by trees and grasses was influenced more by rainfall or by the river water levels.

Findings on browse production in the riparian zone in RNP will fill the knowledge gap on the role of a key resource in rangelands, their contribution in the management of herbivores during the dry season as well the overall impact on sustainable utilization of dry land ecosystems. Study on the variation in forage resource in key resource area in RNP and benefits associated with partitioning of range areas accessible during the rainy and summer seasons is therefore regarded as having important implication in determining the dynamics of herbivore populations. Herbivore populations would be expected to be more stable in ecosystems with spatial resource utilization than would be the case if all resources were exploited continuously throughout the year. This is because spatial variability and accessibility of resources buffer seasonal variability of animal populations by allowing a kind of feed resource refuge to herbivores during droughts.

The aim of this study was to quantify spatial and temporal variations in browse forage production along the Riparian zone during the dry season. The study determined (i) how browse production by woody plant species along the riparian zone in RNP vary between the study sites with time; (ii) the contribution of selected woody plant species to the browse production and (iii) the implication of a dry season key resource in the management of the rangelands. Understanding the responses of herbivores to spatial and temporal heterogeneity of vegetation resource is critical in the design and management of pastoral systems and in the formulation of conservation policies in arid rangelands.

6.3 Materials and methods

6.3.1 Data collection in the riparian zone

Sampling took place at three study sites in the Orange River riparian zone namely Potjiespram, DeHoop and Richtersberg (Figure 6.1a). The three sites were selected because they were the only sites that had a rain gauge and were active (had stock posts where pastoralists had settled with their livestock). In each site, temporal available standing biomass, browse and litter production by the seven dominant tree species (which make up most of the available browse in the riparian zone) were sampled. The tree species sampled were *Ziziphus mucronata*, *Rhus pendulina*, *Euclea pseudebenus, Prosopis glandulosa*, *Acacia karoo, Tamarix usneoides* and *Maytenus linearis.* Data collection took place in the summer (September to April) the period that herbivores utilize the riparian zone to access forage and water.

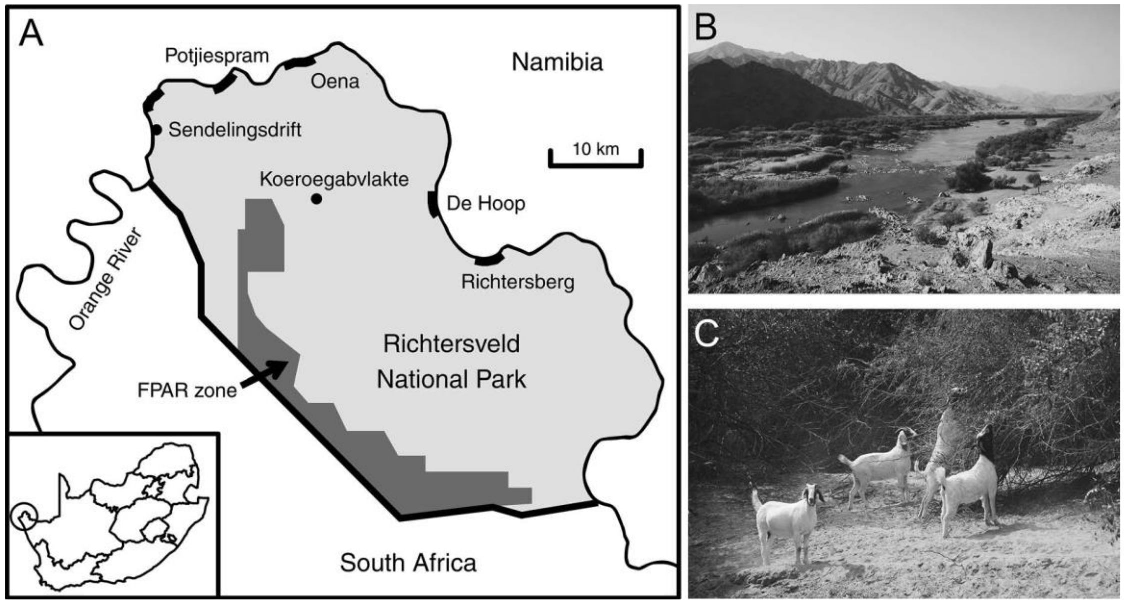


Figure 6.1a-c: Study sites along the riparian zone in RNP

Source: Hempson *et al.,* 2015

6.3.2 Measurement of variation in available standing biomass

The sequence of measuring the available browse to the goats was designed to follow the period (October to April) when the herbivores move to the riparian zone to feed on browse from trees and grasses along the river. Browse production was not measured in winter (May to August) because the goats usually graze on the plains and mountains during this period. The available standing biomass in this case refers to leaves, fruits, flowers and twigs of woody plants below 1.5 m (the height reached by goats). The available standing biomass of browse on branches of seven tree species was estimated by harvesting and branch-count method (Hempson *et al.,* 2015). Branch-count method involved counting the total number of branches on a tree up to a height of 1.5 m then measuring diameter and lengths of sample branches (small, medium and large branches) and harvesting the browse of sample branches on that tree. The browse biomass was harvested manually (Figure 6.2). Before harvesting was done branch length and diameter were measured.

Figure 6.2: Counting and measuring of branches and harvesting of browse forage from the sampled tree branches

The dry mass of the harvested sample branches were multiplied by the total number of branches in each tree to get an estimate of total browse produced per tree canopy up to a height of 1.5 m. The transverse and longitudinal canopy diameters for each sampled tree were measured (in metres) and used to calculate canopy areas. The two diameters of the tree canopies were used to calculate the canopy area using the formula $\{(\pi * D_1 * D_2) /4\}$ as described by van der Vyer *et al.*, (2019). To calculate browse production per square meter the browse produced per tree canopy was divided by the tree canopy area (Tollenson *et al.*, 2019).

Counting and harvesting of branches were done after every two months (in September 2006, November 2006, January 2007 and April 2007, November 2007 and April 2008) representing the entire summer period. Browse harvested at the onset of the summer period (in September) were considered as the peak total standing biomass on the branches before any browsing has taken place while the differences between browse harvested in different times of the year were considered as the amount browsed by the goats.

6.3.3 Measurement of browse production

In each study site, six representatives of each tree species were selected and enclosed by a fence to keep off browsing by goats. The canopy diameters (transverse and longitudinal) of the enclosed trees and the number of branches below 1.5 m were recorded. In the fenced enclosure, sample branches representing small, medium and large branches were harvested at the start of the summer period (September). The same branches were re-harvested after every two months to quantify the re-growth of leaves per branch and total re-growth per tree. The total dry mass of the harvested sample branches were multiplied by the total number of branches in each tree to get an estimate of total browse produced per tree canopy.

6.3.4 Measurement of litter production from trees

Litter fall contributes a substantial amount of forage to herbivores in RNP especially when the browse is dwindling in the lower canopy and only available at a height that animals cannot reach (personal observation). Under each enclosed tree in each study site, a litter trap was placed to collect the litter (leaves, flowers, fruits and twigs) that fall from the tree (Figure 6.3). The exclosure kept the animals from interfering with the litter traps. The litter traps were emptied after every 2 months, separated into leaves, fruits, flowers and twigs, dried at 70°C for 48 hours and weighed separately.

Figure 6.3: A litter trap placed under an enclosed woody plant canopy to collect leaves, twigs and litter

6.3.5 Measurement of grass biomass production

Grass in RNP was found in patches along the Orange River banks. Grass cover stretch along the riparian zone as shown in Figure 6.6a-b. To measure grass biomass production, transects of I km long parallel to the river were measured at each site. 1 m x 1 m plots were measured, and grass was harvested. 1 m x 1 m mobile cages were used to keep off animals from grazing. The grass forage in the cages was clipped after every two months and cages were re-located. In addition, 1m x 1m plots were measured outside the cages and the grass within these plots was clipped to the ground level. Clipping of grasses in grazed and un-grazed plots was done simultaneously in September 2006, November 2006, January 2007, November 2007, January 2008 and April 2008. All the harvested grass was packed in polythene bags, oven dried and weighed.

6.3.6 Orange River water level data in RNP

The impact of floods along the Orange River on forage availability was assessed through continuous monitoring of the river water levels and measuring the amount of grass available to the goats during the low and high river water levels. The Orange river water level data that were obtained from Department of Water and Forestry (DWAF) head office and were used as indicators of the surface water discharge at different times of the year corresponding to the same period when sampling of grass biomass was carried out (that was in September 2006, November 2006, January 2007, November 2007, January 2008 and April 2008). The availability of grasses to animals along the Orange River depended on the river water flood levels. When the grasses were covered by water, the animals could not access them and therefore grasses were only available forage when the river water levels were low. The flow of river water did not originate only from the park, but from the larger Richtersveld region.

6.3.7 Rainfall Data

Monthly rainfall data that were recorded in RNP in the five rain gauges found in the park, were obtained from the South African Weather Service.

6.4 Data Analysis

Linear regression analysis was performed to test the relationship between the length and diameter of branches with harvested biomass. The harvested browse and respective branches parameters for the peak season (September) were used in linear regression analysis as the best representative of peak biomass of all tree species before any browsing had taken place.

To calculate the total biomass production per tree canopy area, branch count method was used. This involved multiplying the number of branches below 1.5 m by the browse production of the harvested sample branches. The two diameters (diagonal and transverse) of the tree canopies were used to calculate the canopy area.

To calculate browse production per square meter the browse produced per tree canopy was divided by the tree canopy area. Forage browsed by goats were considered as the differences between browse productions at the beginning of the summer period (September) minus the amount of forage that was available on the branches at the subsequent sampling period (after every 2 months). The dry mass of litter produced in each tree species per canopy area was determined by adding together litter that was collected in the trap throughout the summer period.

Repeated measure ANOVA was used to analyse the amount of litter produced per tree species as well as the contribution of leaves, fruits, flowers and twigs to the total litter production. Factorial ANOVA was used to test for the effect of sites, sampling period and species at significance level of 95 percent significance levels of available browse, litter and browse production.

6.5 Results

6.5.1 Measurement of available standing biomass

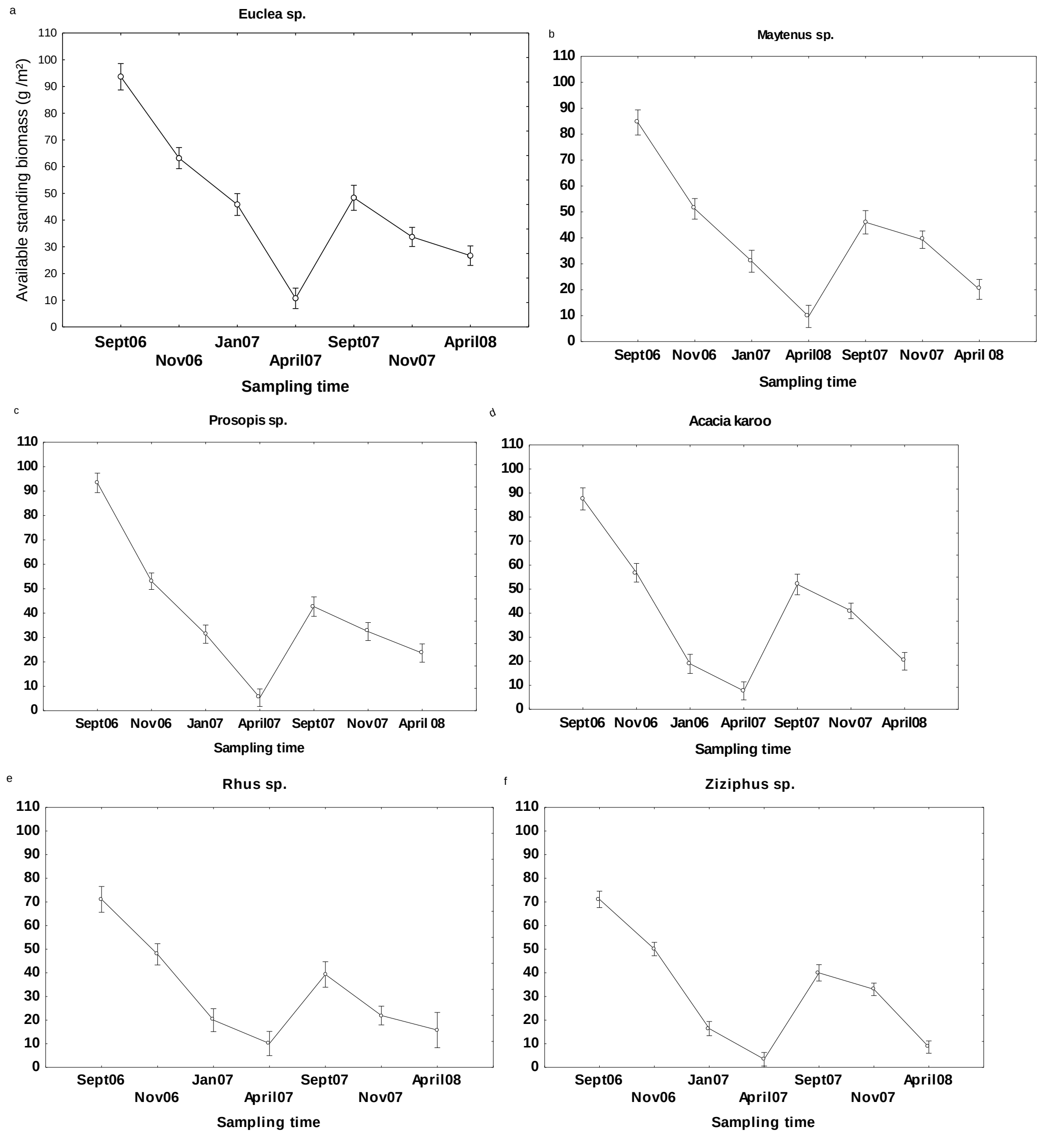
Regression equations between total available biomass and branch dimensions (diameter and length) were developed for each tree species as shown in Table 6.1. Regression equation between browse biomass and stem diameter showed that *E. pseudebenus* had the highest R^2 value of 0.79 followed by *R. pendulina* 0.78, *P. glandulosa* 0.74 and *M. linearis*. 0.74. *T. usneoides* had the lowest R^2 value of 0.61. Regression equation between available browse biomass and branch length show that *Z. mucronata* had the highest R^2 value of 0.80, followed by *A. karoo* 0.74, R. *pendulina* 0.73 and *P. glandulosa* 0.72. *T. usneoides* had the lowest R^2 value of 0.62 (Table 6.1). The regression equations of different tree species were used to estimate the total available browse production of each species at a height of 1.5 meters (the height at which forage was available to goats).

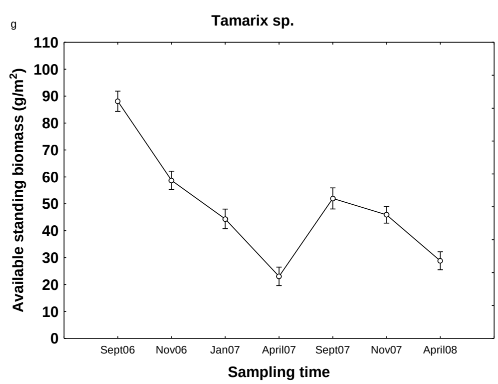
Table 6.1: Regression equations between total available browse biomass and branch dimensions for each tree species

Species	Branch diameter vs biomass		Branch length vs biomass	
	R^2	Equations	R^2	Equations
A. karoo	0.66	y = 2.696x + 20.34	0.74	y = 31.36x + 13.82
E. pseudebenus	0.79	y = 3.292x + 22.28	0.71	y = 34.25x + 22.84
M. linearis	0.74	y = 3.271x + 16.39	0.67	y = 31.31x + 19.51
P. glandulosa	0.74	y = 3.184x + 22.0	0.72	y = 32.50x + 21.87
R. pendulina	0.78	y = 3.096x + 15.36	0.73	y = 31.59x + 15.84
T. usneoides	0.61	y = 2.645x + 34.38	0.62	y = 32.01x + 28.91
Z. macrunata	0.67	y = 2.611x + 21.08	0.80	y = 30.65x + 16.73

6.5.2 Temporal variation in available browse during the two summer periods

The available standing biomass was higher at the beginning of summer in the month of September in 2006 and 2007 for the tree species (figure 6.4a-g). The available standing biomass of forage reduced with time because of the removal by goats and was lowest in April, the end of summer period. *E. pseudebenus* and *P. glandulosa* had the highest available standing biomass at the beginning of summer periods before any browsing had taken place (Figure 6.4a-g). The most fed on tree species showing much decline in browse from onset of summer in September to end of summer period in April were *Z. mucronata, R. pendulina, A. karoo, Prosopis glandulosa, E. pseudebenus, M. linearis* and *T. usneoides respectively* (Figure 6.4a-g).





(Abbreviations - Acacia sp. is *Acacia karoo*, Euclea sp. is *Euclea pseudebenus*, Maytenus sp. *is Maytenus linearis*, Prosopis sp. *is Prosopis glandulosa*, Rhus sp. *is Rhus pendulina*, Tamarix sp. *is Tamarix usneoides* and Ziziphus sp. is *Ziziphus mucronata*

Figure 6.4 (a-g): Temporal variation in available browse during summer period from September 2006 to April 2008 of the seven tree species

Available standing biomass differed significantly between the species ($p<0.05$; $F_{(5, 676)}= 69.38$) and between sampling seasons ($p<0.05$; $F_{(5, 676)}=1299.7$) but did not differ significantly between sites ($p>0.05$; $F_{(1, 676)}=0.005$) as shown in table 6.2. There was a significant interaction between sampling time and different tree species, sampling time with sites. Also there was a significant interaction between sites and species (Table 6.2).

Table 6.2: Level of significance in available standing biomass for the period September 2006 to April 2008

Effects	P-value	F-value
Species	<0.05	$F_{(5, 676)}= 69.38$
Sampling time	<0.05	$F_{(5, 676)}= 1299.7$
Sampling time x Species	<0.05	$F_{(35, 676)}= 7.41$
Sites	>0.05	$F_{(1, 676)}= 0.005$
Sites x Species	<0.05	$F_{(11, 676)}= 2.35$
Sampling time x Sites	>0.05	$F_{(11, 676)}= 0.56$

6.5.3 Measurement of spatial and temporal browse production

Browse production in this case refers to forage produced by tree species after every two months (between November 2006 and April 2008). Results presented in Table 6.3 show that browse production was significantly different among the 7 tree species ($p<0.05$; $F_{(6, 84)} =5.61$), in different sampling time ($p<0.05$; $F_{(5, 84)}=11.14$) and between the three study sites ($p<0.05$; $F_{(2, 105)}=3.43$). Browse production was also significantly different between the two years 2006 and 2007

($p<0.05$; $F_{(1, 112)}=5.36$). There was a significant difference between browse production in different study sites and species ($p<0.05$; $F_{(12, 105)}=3.10$), sampling time with species ($p<0.05$; $F_{(30, 84)}=0.49$) but there was no significant interaction of sampling time with sites as well as years with species (Table 6.3)

Table 6.3: Variation in browse production between September 2006 and April 2008

Effects	P-value	F-value
Species	<0.05*	$F_{(6, 84)}= 5.61$
Sampling time	<0.05*	$F_{(5, 84)}= 11.13$
Sites	<0.05*	$F_{(2, 105)}= 3.43$
Sites x Species	<0.05*	$F_{(12, 105)}=3.10$
Sampling time x Species	<0.05*	$F_{(30, 84)}= 0.49$
Sampling time x Sites	>0.05	$F_{(10, 108)}= 0.65$
Study years	<0.05*	$F_{(1, 112)}= 5.36$
Study years x Species	>0.05	$F_{(6, 112)}= 0.35$

There was significant difference between browse production in the 3 study sites ($p<0.005$; $F (2, 105) = 3.10$) as shown in Figure 6.5. Browse production by *A. karoo, R. pendulina*, *E. pseudebenus* and *Z. mucronata* was significantly different between the 3 study sites (Figure 6.5). Browse production by *P. glandulosa* was significantly lower in Richtersberg but there was no significant difference in browse production between Poijispram and DeHoop sites. Browse production by *T. usneoides* was significantly higher in Richtersberg but was not significant different between the other two study sites. Browse production by *M. linearis* was significantly higher in DeHoop but was not significantly different between Poikiespram and Richtersberg (Figure 6.5).

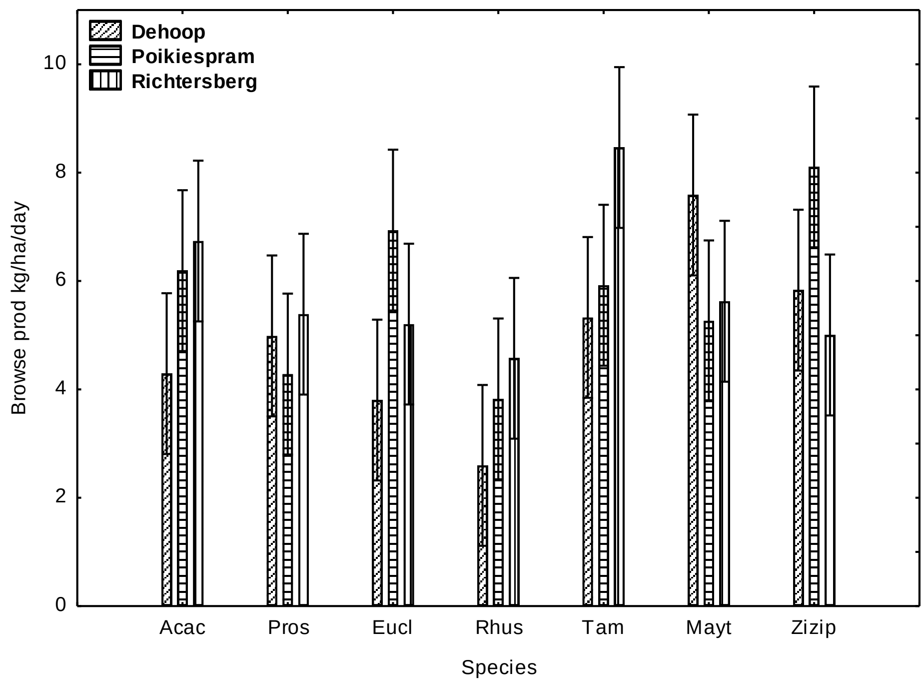


Figure 6.5: Variation in browse production between the 3 study sites

The abbreviated trees species are*: A. karoo, P. glandulosa, E. pseudebenus, R. pendulina, T. usneoides M. linearis,* and *Z. mucronata)*

6.5.4 Measurement of litter production by different tree species

Litter from the 7 tree species contribute to the total browse available to goats in RNP. Litter production differed significantly between the tree species ($p<0.05$; $F_{(6,}$

$_{13)}$=69.87) and between sampling time ($p<0.05$; $F_{(5, 85)}=4.68$) but did not vary between sites ($P>0.05$) as shown in Table 6.4. There was significant difference in browse production by different species with sampling time ($p<0.05$; $F_{(30, 65)}=5.96$) but there was no significant difference ($P>0.05$) between study sites and sampling time (Table 6.4).

Table 6.4: Level of significance for the total litter production between species, sites and sampling time

Effect	P-value	F-value
Species	<0.05	$F_{(6, 13)}=69.87$
Sites	>0.05	$F_{(2, 17)}=0.42$
Time (Sampling time)	<0.05	$F_{(5, 85)}=4.68$
Species x Time	<0.05	$F_{(30, 65)}=5.96$
Sites x Time	>0.05	$F_{(10, 85)}=0.74$

Litter production by *A. karoo* was significantly higher than the other tree species (Figure 6.6). *R. pendulina* produced the lowest amount of litter compared to the other tree species. However there was no significant difference in litter production by *P. glandulosa, Z. mucronata,* and *E. pseudebenus* tree species although it was higher than the litter produced by *M. linearis* and *T. usneoides* species (Figure 6.6). Litter production differed significantly between sampling time (Figure 6.7) whereby there was more litter production in the month of September 2006 and November 2007 by all tree species. There was low litter production in January 2007 and in April 2008 by all tree species (Figure 6.7 and 6.8). Abbreviated tree species are *A. karoo, P. glandulosa E. pseudebenus, R. pendulina, T. usneoides M. linearis,* and *Z. mucronata.* Different letter shows significant difference while same letter shows no significance difference. Vertical bars denote 0.95 confidence intervals.

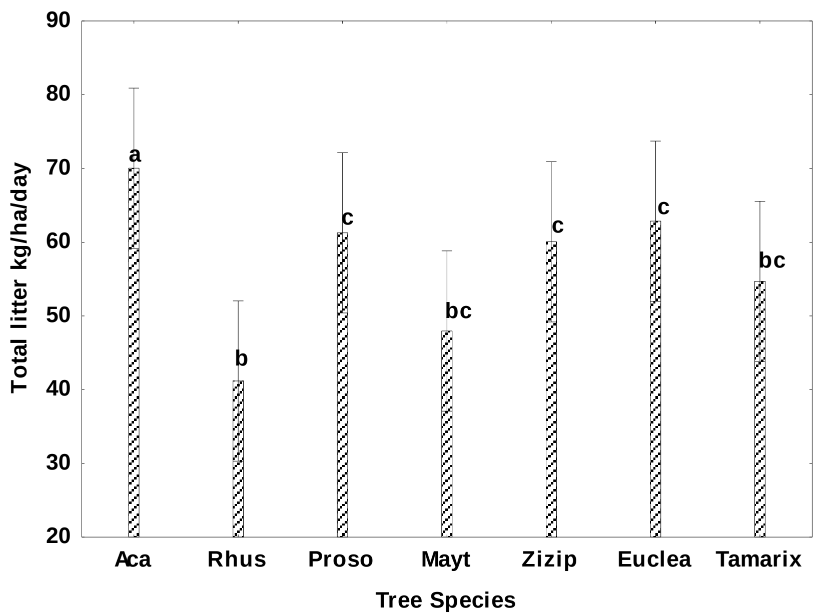


Figure 6.6: Total litter production by different species

Different letter shows significant difference while same letter shows no significance difference. Vertical bars denote 0.95 confidence intervals.

Leaves contributed the highest percentage of litter component followed by twigs while fruits and flowers contributed lower percentage. Leaves of *T. usneoides* 59.8%, *P. glandulosa* 55%, and *M. linearis* 54.9% species had the highest percentage contribution to the total amount of litter. *E. pseudebenus*, *Z.mucronata* and *P. glandulosa* species contributed the highest amount of fruits in the litter respectively. *A. karoo*, *E. pseudebenus*, and *R.s pendulina* speci es produced the highest amount of flowers respectively while *T. usneoides*, *M.s linearis*, *A. karoo* and *E. pseudebenus* produced the highest amount of twigs component of the litter.

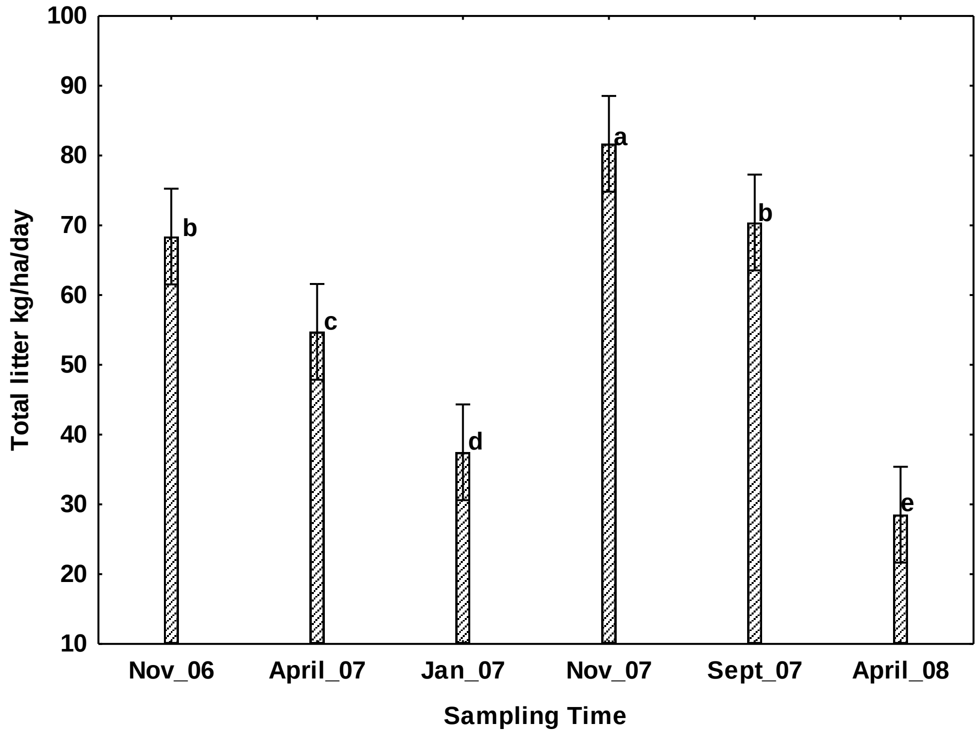


Figure 6.7: Temporal variation in total litter production

Leaves contributed the highest proportion of the litter in all the 7 tree species, while fruits and flowers contributed the lowest amount of litter component in most tree species (Figure 6.9).

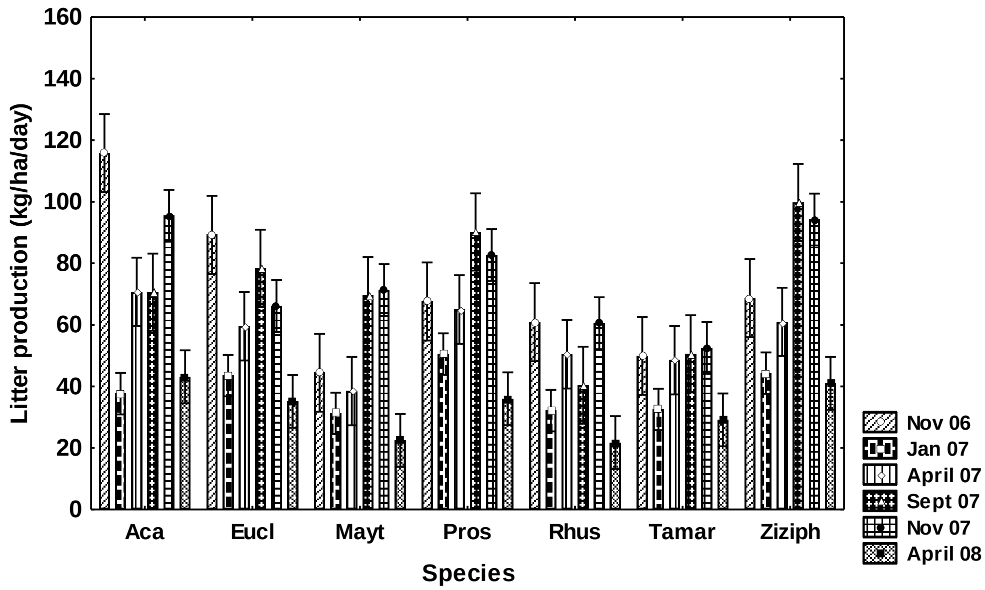


Figure 6.8: Litter produced by different species at different sampling times of the year

Abbreviated tree species are - The abbreviated tree species: - *A. karoo, R. pendulina P. glandulosa, M. linearis Z. mucronata, E. pseudebenus,* and *T. usneoides*

Litter production differed significantly between the tree species and between sampling time but did not vary between sites and between sampling time**.** Litter production by *A. Karoo* was significantly higher than the other tree species. *R. pendulina* produced the lowest amount of litter compared to the other tree species. However there was no significant difference in litter produced by *P. glandulosa, Z. mucronata*, and *E. pseudebenus* tree species although it was higher than the litter produced by *M. linearis* and *T. usneoides* species. Litter production differed significantly between sampling time whereby there was more litter production in the month of November, 2006 and September and November 2007 by all tree species. There was low litter production in January 2007 and in April 2008 by all tree species.

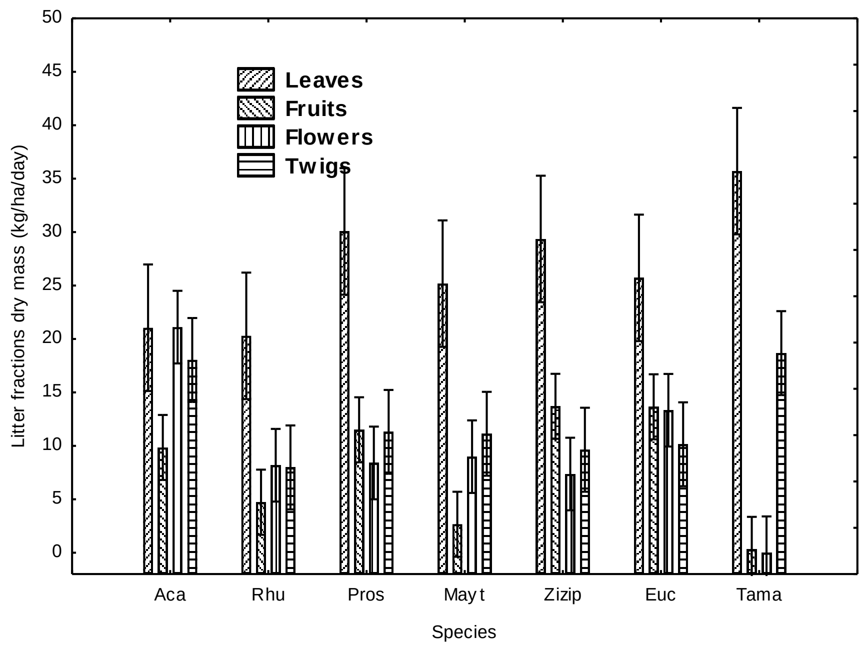


Figure 6.9 Contribution of different litter components from different tree species to the total litter production

Vertical bars denote 0.95 confidence intervals. The abbreviated tree species: - *A. karoo, R. pendulina P. glandulosa, M. linearis Z. mucronata, E. pseudebenus,* and *T. usneoides.*

6.5.5 Grass biomass production along the Orange River

River water levels were found to have a positive correlation with grass biomass production ($p<0.05$) while sampling period/month and rainfall had no effect on grass biomass production (Table 6.5). Interaction between grass biomass and river water levels as well as interaction between grass biomass production and rainfall had positive correlation at P<0.05 as shown in Figure 6.6.

Table 6.5: Influence of river water levels and rainfall on grass biomass production and availability

Intercept	**df**	**F-ratio**	**P-value** (< 0.05)
River water levels	1	3.90	<**0.05***
Grass Biomass vs River water levels	1	240.6	<**0.05***
Sampling period	1	5.60	>0.05
Grass Biomass vs time	1	3.32	>0.05
Rainfall	1	2.30	>0.05
Grass Biomass vs rainfall	1	629.40	<**0.05***
Sampling sites	1	0.04	>0.05
Grass Biomass vs sites	1	0.31	>0.05

River water levels were found to be low in the months of September in 2006 and in April in 2007 and 2008 (Figure 6.10 and Figure 6.11). On the other hand, river water levels were higher in the months of November in 2006 and January and November in 2007. Figure 6.10 shows that during summer periods the river water levels would subside allowing the grass to grow and be available forage to goats and therefore during the high rainfall seasons there was low grass biomass production while on the dry seasons in summer there was high grass biomass production in RNP riparian zone as shown in Figure 6.11. River water levels were found to have a significant influence on grass forage production and availability. In September 2006 the riparian zone produced (600 g/m^2), April

2007 (650 g/m^2), November 2007 (650 g/m^2) and in April 2008 (700 g/m^2) that was accessible by goats because the river water levels were below 20 m^3. On the other hand from November 2006 to March 2007 and also in November 2007, the river water levels were very high above 40m^3 and therefore the grass was inaccessible to goats because of floods as shown in Figure 6.11 . Rainy seasons were in months of April to July while dry seasons were in September to March (Figure 6.11)

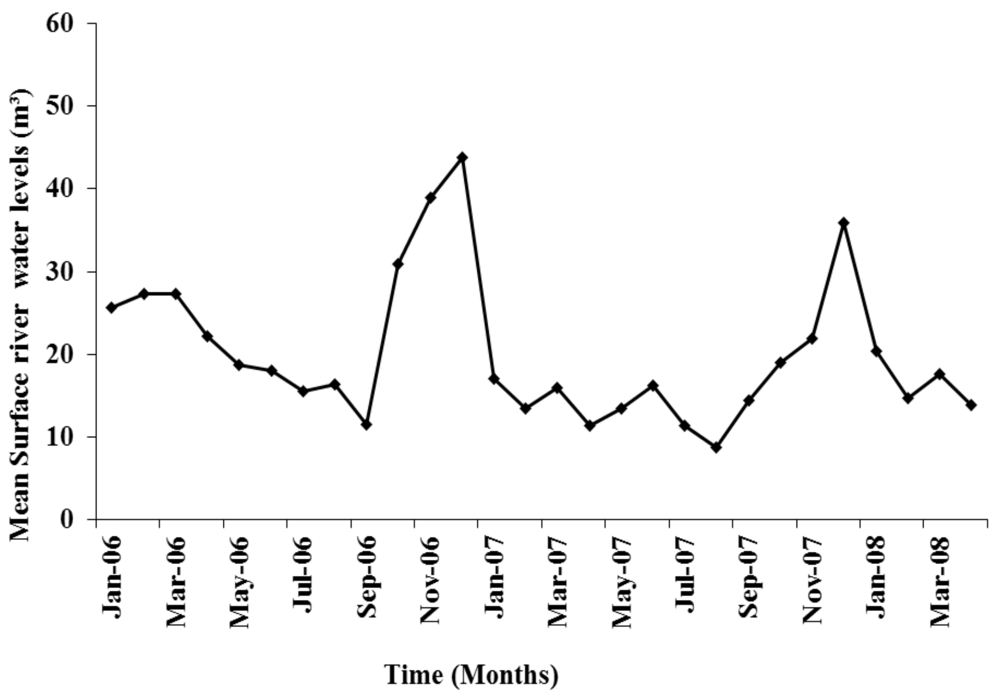


Figure 6.10: Orange River surface water levels (m³) in RNP

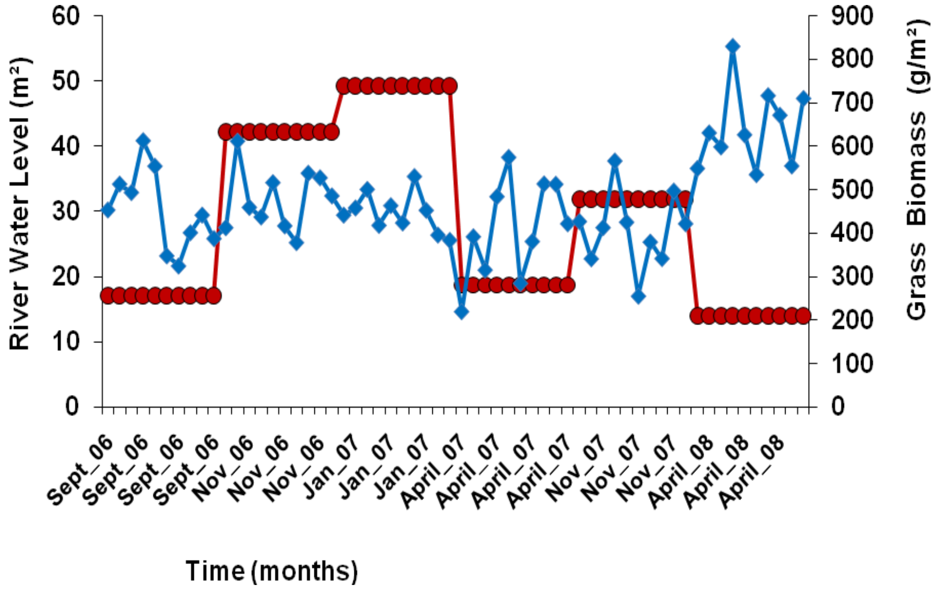


Figure 6.11: Influence of rainfall and river water levels on grass biomass production

(●●●- represent river water levels in **m**³ while ♦♦♦ - represent grass biomass in **g/m**²)

6.6 Discussion

6.6.1 Spatial and temporal browse production

Browse from trees along the riparian zone in RNP was found to bridge the gap of forage availability during the dry seasons. To partition and maximize resource use, pastoralists in RNP spend the entire summer period along the Orange River (September to April) so that animals can feed on browse and grass along the riparian zone and then move to the plains and mountains in the remaining four months in winter period when there is availability of herbaceous plants and shrubs.

Use of allometric relationship between stem length and diameters with available biomass on branches in RNP showed very good fits. The study showed a strong positive correlation between stem length and diameter with available standing browse (R^2 of 0.61 to 0.8). Use of allometric models were more effective, less destructive and not labour intensive. The research findings show that browse production fluctuated between and within years and among the seven woody plant species. This was consistent with other studies that reported variation in browse resource availability in rangelands depending on plant species (Hempson *et al.*, 2015; Mukeka *et al.*, 2019).

Of the seven woody species found in RNP, Z. *mucronata, R. pendulina, A. karoo, P. glandulosa* were found to contribute to forage and were more preferred by herbivores while *E. pseudebenus, T. usneoides* and *M. linearis* were less preferred. Figure 6.1a-g.show that the amount of browse production (at a height of 1.5 m) reduced with time in dry period from September to April. Reduction of browse on tree branches due to browsing by goats was higher in *Z. mucronata, R. pendulina, A. karoo, P. glandulosa* respectively while on the other hand; minimal reduction in available browse was recorded in *E. pseudebenus, T. usneoides* and *M. linearis.* Woody plant species that recorded drastic reduction of browse on the branches at a height of 1.5 m and below were considered as the most preferred source of forage than those species that recorded less reduction in available browse with time. The findings were consistent with study by Hempson *et al.*,

(2015) that reported positive correlation between browsing of *Z. mucronata, R. pendulina* and *A. karoo* with increase in adult goat density, and *Z. mucronata* and *R. pendulina* being the most preferred browse species in RNP.

Available standing biomass differed significantly between the species, but did not between sites as shown in Figure 6.2. Although *Z. mucronata*, *R. pendulina, A. karoo,* and *P. glandulosa* were the most preferred species for browsing by goats, on the other hand it was *E. pseudebenus, T. usneoides* and *P. glandulosa* that had the highest browse production. This therefore shows that not all forage available in the study sites was of benefit to the animals. In RNP goats were found to avoid feeding on the browse of *E. pseudebenus*, *T. usneoides* and *M. linearis* despite the fact that the three species do not have morphological deterrents such as thorns.

From other studies leaves of some woody species are associated with high concentration of secondary metabolites (Otieno *et al.*, 2019) and thus not consumed by animals. For *P. glandulosa* that was very dominant in riparian zone in RNP, goats were found to prefer feeding mostly on their legume seed pods than on leaves (personal observation). The bean-like pods of *P. glandulosa* have been documented as nutritious food source for wildlife and livestock.

Z. mucronata was the most fed on species, its fruits and leaves were a valuable fodder source for the goats. This was in agreement with Hempson *et al*. (2015).

Z. mucronata was followed by *R. pendulina, Acacia karoo* and *P. glandulosa* respectively. Three out of the four most preferred species had thorns presumably for defence against browsing. This was in agreement with findings by Otieno *et al.,* (2019) who found that plants that were very thorny had less concentration of tannin content compared to thorn-less species that were tannin-rich. In this study woody species that were browsed more such as *Z. macronata, Acacia karoo* and *P. glandulosa* have thorns (except *R. pendulina*) while woody species that were not preferred for browsing (*E. pseudebenus, T. usneoides* and *M. linearis)* had no thorns.

Another observation was that there was no significant difference between the total browse production in the 3 study sites (Poijispram, DeHoop and Richtersberg), although different species produced slightly higher or lower browse in some sites compared to others. This may be attributed to uneven distribution of the 7 woody species found in the 3 study sites in RNP. Litter fall mainly from the top canopies in form of leaves, fruits, flowers and twigs contributed substantial amount of forage to herbivores in RNP especially when the browse was dwindling in the lower canopy and was only available at top canopy where animals could not reach.

Leaves and twigs contributed the highest amount of litter compared with fruits and flowers. Out of the 6 woody species, *Acacia karoo* contributed the highest amount of litter. Depending on browse preference for each species, the study therefore shows that fruits from *Z. mucronata* and *P. grandulosa* contributed the highest amount of palatable litter, followed by flowers of *A. karoo* and *R. pendulina* This may be attributed to the earlier observations in the depletion of available browse on branches of the 7 species, that herbivores in RNP had less preference for browse from thorn-less species such as *E. pseudebenus, T. usneoides,* and *M. linearis* that produced higher amount of twigs and leaves as litter.

Other studies have also shown that leaves from upper canopy have less metabolites compared to leaves from lower canopy as a defence mechanism from browsing pressure (Otieno *et al*., 2019). This may lead to animals feeding on litter that fall from top canopy due to low level of metabolites while at the same time avoiding browsing on leaves of the same species that at the lower parts of the plant. According to Naah and Guuroh (2017), study of spatial and temporal variation in forage production coupled with pastoralists' local knowledge on forage variability would help in sustainable resource utilization, environmental management and livestock production in rangelands such as RNP.

6.6.2 Grass forage production species in the riparian zone in RNP

The study showed that in the period when the water levels were low, there was high grass biomass available and accessible to herbivores for grazing, unlike during winter seasons when the grass was covered with water thus not accessible to herbivores. During summer periods the river water levels would subside allowing the grass to grow and be available forage to goats. During the high rainfall seasons there was low grass biomass production while on the dry seasons in summer there was high grass biomass production in RNP riparian zone. Orange River riparian zone play a key role in sustaining forage availability during the dry seasons. The pastoralists' value this key resource area because it acts as a refuge during the dry seasons for the provision of water, shade and forage.

CHAPTER 7: SYNTHESIS OF FINDINGS, CONCLUSION AND RECOMMEDATIONS

7.1 Introduction

The purpose of this study was to determine whether biomass production, species composition and diversity of annual plants were positively correlated with rainfall, grazing and soil nutrients. The study found that there was a stronger positive correlation between abiotic factors such as rainfall with forage production and distribution than with biotic factors (grazing, soil nutrients and landforms) in RNP.

The results were also in agreement with the hypothesis that there was spatial and temporal variation in forage production both in the dry season key resource (Riparian zone) and in the wet season resource areas (on the plains, foothills and mountains), but the variation was greater during the dry season than during the rainy season. Variation in forage on the plains, foothills and mountains was dictated more by rainfall than grazing. On the other hand, spatial and temporal variation in forage production in the key resource area along the river was influenced more by grazing pressure due to height effect as herbivores could only browse forage up to a height of 1.5 m.

The study confirmed the ecological theories that forage production in dry ecosystems are not uniform, they vary in space and time due to the effect of various biotic and abiotic ecological factors. Leaf and stem succulents plants were found to contribute more to the total biomass production on RNP than non-succulents and grass species. Also forage production by browse tree species also differed with time and with species preference by herbivores (goats and sheep). From the seven tree species that were sampled along the riparian zone, four species (*Z. mucronata, R. pendulina, A. karoo* and *P. grandufolia*) were browsed more than the other 3 tree species (*T. usneoides* and *M. linearis*); although forage production by the seven tree species did not vary between the study sites. This may be due to the similarity in ecological and edaphic factors among the study sites along the river. The study advocate for herbivores mobility in the study area so that pastoralists can take advantage of the observed spatial and temporal variation inforage production between the landscapes and seasons in RNP

7.2 Conclusions

The study showed that in RNP:

(i) Abiotic factors such as rainfall drives the primary productivity, plant species richness, diversity, composition and distribution more than biotic factors such as grazing, landforms and soil variables.

(ii) Rainfall influenced biomass production by shrubs as well as the composition and distribution of perennial plants in RNP. Biomass production by shrubs as well the remote sensing fpar values had a strong correlations with rainfall. This means rainfall data and remote sensing data are effective tools that can be used to estimate biomass production in rangelands.

(iii) There was difference between the spatial and temporal variation in forage production in the dry season forage resource compared to the wet season resource. There was uncoupling of herbivores numbers with forage availability during the rainy season in a density-independent manner. This was in agreement with findings by Hempson *et al.*, (2015).

(iv) The herbivores did not exploit all the forage resources that were available in the flat plains, foothills and mountains during the wet seasons. This was in support of existence of a non-equilibrium dynamic in RNP ecosystem. On the other hand, during the dry season along the riparian zone, forage resource from trees reduced with time, and due to height effect, goats and sheep could reach forage up to a height of 1.5m. Therefore there was coupling of forage resources with herbivores with time as dry period continued. This was in support of an occurrence of an equilibrium dynamic in the riparian zone. The dynamics differed during the wet and dry seasons in RNP.

7.3 Recommendations

The following were the recommendations:

7.3.1 Recommendation for management actions

(i) Frequent monitoring of spatial and temporal forage hot spots in the study area using modern technologies such as MODIS and satellite images should be encouraged. Frequent geospatial analysis can help in tracking of forage availability and even utilization of landscapes in rangelands globally.

(ii) Globally, joint rangeland management by government and local communities should be encouraged and implemented for an effective community-based management of natural resources in order to balance the social and economic benefits of pastoralists and biodiversity conservation.

7.3.2 Recommendation for further studies

(i) 1. Studies should be conducted on the nutritive value of browse forage from different woody plants available in riparian zone in RNP which serve as supplements of forage during the dry season should be to confirm the reasons why there was variance in their preference by herbivores.

(ii) Studies are recommended to establish the actual levels of deterrent secondary metabolites and digestibility levels of these woody species found in NRP in relation to animal preference in browsing.

(iii) There is need to carry out an integrated Ecological Modelling to find how the various biotic (rainfall, temperature) and abiotic factors (grazing intensity, soil variables, landforms) influence forage biomass production and animals dynamics in RNP.

7.3.3 Recommendations for policy interventions

(i) Park managers should come up with management policies that will review introduction of additional stock posts and herbivores numbers in the park in order to control the effects of grazing on plants and soil in the park due to the observed piosphere effects near the stock posts.

(ii) Management policies in RNP should embrace herd mobility strategies and landscapes stratification whereby herbivores utilize certain areas at specific time of the year so as to benefit from the forage resource heterogeneity and to mitigate negative effects of climate variability on herbivores and range condition not only in RNP but in all other rangelands globally.

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APPENDICES

Appendix 1: List of plant species encountered in RNP during the study

S.no	Plant Species	Families
1	*Acanthopsis disperma* Harv.	Acanthaceae
2	*Acanthopsis carduifolia* (L.f.)Schinz	Acanthaceae
3	*Justicia betonica* L.	Acanthaceae
4	*Aizoon canariensis* Linn.	Aizoaceae
5	*Aridaria noctiflora* (L.)Schwantes	Aizoaceae
6	*Aspazoma amplectens* (L.Bolus) N.E. Br.	Aizoaceae
7	*Astridia longifolia (*L.Bolus) L.Bolus	Aizoaceae
8	*Astridia vanheerdei* L.Bolus	Aizoaceae
9	*Brownanthus arenosus* (Schinz) Ihlenf.& Bittrich	Aizoaceae
10	*Brownanthus pseudoschlichtianus* S.M Pierce &Gaubaulet	Aizoaceae
11	*Cheiridopsis denticulate* (Haw.) N.E.Br.	Aizoaceae
12	*Cheiridopsis robusta* (Haw.) N.E.Br.	Aizoaceae
13	*Drosanthemum diversifolium* L.Bolus	Aizoaceae
14	*Eberlanzia dichotoma* (L.Bolus)H.E.K.Hartmann	Aizoaceae
15	*Galenia africana L.*	Aizoaceae
16	*Mesembryanthemum barklyi* N.E. Br.	Aizoaceae
17	*Mesembryanthemum guerichianum* Pax.	Aizoaceae
18	*Mesembryanthemum nodiflorum L.*	Aizoaceae
19	*Prenia sladeniana (*L.Bolus*)*L.Bolus	Aizoaceae
20	*Prenia tetragonia* (Thunb.)Gerbaulet	Aizoaceae
21	*Ruschia lineolata* Schwantes	Aizoaceae
22	*Ruschia pulvinaris* L.Bolus	Aizoaceae
23	*Stoeberia beetzii* (Dinter)Dinter &Schwantes	Aizoaceae
24	*Stoeberia utilis (*L.Bolus) van Jaarsv.	Aizoaceae
25	*Trianmthema parvifolium* E.Mey ex Sond.	Aizoaceae
26	*Rhus pendulina* Dr.J.P. Roux	Anacardiacae
27	*Leipoldtia schultzei* (Schltr.& Diels)	Asparagaceae
28	*Bulbine frutescens* (L.)Wild	Asphodelaceae
29	*Trachyandra bulbifolia*	Asphodelaceae

30	*Trachyandra muricata* (L.f) Kunth.	Asphodelaceae
31	*Amellus nanus* DC.	Asteraceae
32	*Berkheya spinosissima* (Thunb.) Willd	Asteraceae
33	*Cotula barbata* DC.	Asteraceae
34	*Cotula obtuse* L.	Asteraceae
35	*Cotula toneifolia* L.	Asteraceae
36	*Didelta carnosa* (L.F.)Aiton	Asteraceae
37	*Dimophotheca tragus* (Aiton) B.Nord	Asteraceae
38	*Dimorphotheca polyptera* DC.	Asteraceae
39	*Dimorphotheca sinuata* DC.	Asteraceae
40	*Felicia australis* (Alston)E.Phillips	Asteraceae
41	*Felicia brevifolia* (DC) Grau.	Asteraceae
42	*Felicia dubia* Cass.	Asteraceae
43	*Felicia merximuelleri* Grau.	Asteraceae
44	*Gazania lichtensteinii* Less.	Asteraceae
45	*Gazania tenuifolia Less*.	Asteraceae
46	*Geigeria ornativa O.Hoffm.*	Asteraceae
47	*Gorteria diffusa* Thunb.	Asteraceae
48	*Gorteria personata* Hill	Asteraceae
49	*Grileum humanism Thunb*.	Asteraceae
50	*Helichrysum arenaruim* (L.) Moench	Asteraceae
51	*Helichrysum leontonyx* Leontonyx DC.	Asteraceae
52	*Helichrysum nitens* Oliv.& Hiern	Asteraceae
53	*Helichrysum stellatum* Mill.	Asteraceae
54	*Helichrysum tinctum* Thunb.	Asteraceae
55	*Hirpicium echinus* Less.	Asteraceae
56	*Lasiospermum brachyglossum* DC.	Asteraceae
57	*Oncosiphon grandiflorum*	Asteraceae
58	*Oncosiphon pilulifer* (L.F.) Kallersjo	Asteraceae
59	*Oncosiphon suffruticosum* (L.) Kallersjo	Asteraceae
60	*Osteospermum granduflorum* (Phill.)T.Nort.	Asteraceae
61	*Osteospermum pinnatum* Phill.)T.Nort.	Asteraceae
62	*Othonna cylindrical* (LAM.)DC.	Asteraceae
63	*Othonna protecta* Dinter	Asteraceae
64	*Othonna capensis* L.H.Bailey	Asteraceae
65	*Othonna arbuscula (*Thunb.)Sch.Bip.	Asteraceae
66	*Pentizia incana* (Thunb.)Kuntze	Asteraceae
67	*Pentizia dentate* (L.) Kuntze	Asteraceae

68	*Phyllobius nitidus* L.A	Asteraceae
69	*Senecio glaucus L.*	Asteraceae
70	*Senecio barbertonicus* Klatt	Asteraceae
71	*Ursinia cakilefolia* DC.	Asteraceae
72	*Ursinia chrysanthemoides (*Less.)Harv.	Asteraceae
73	*Ursinia calenduliflora (*DC.)N.E.Br	Asteraceae
74	*Amsinckia retrorsa* Suksd.	Boraginaceae
75	*Codon royenii* L.	Boraginaceae
76	*Heliophila carnosa (*Thunb.) Steud	Brassicaceae
77	*Heliophila trafurca* Burch. Ex DC.	Brassicaceae
78	*Dryerophytum africanum* L.	Caesalpiniaceae
79	*Wahlenbergia prostrata* A. DC.	Campanulaceae
80	*Cleome foliosa* Hook.f.	Capparaceae
81	*Maytenus linearis* L.f Marais	Celastraceae
82	*Ornithoglossum viride* (L.F)Dryand.ex.W.T.Aiton	Colchicaceae
83	*Ornithoglossum vulgare* B.Nord.	Colchicaceae
84	*Crassula macowaniana* Schonl.&Baker,f	Crassulaceae
85	*Tylecodon wallichii (*Harv.)Toelken	Crassulaceae
86	*Euclea pseudebenus* Dr.J.P. Roux	Ebenaceae
87	*Euphorbia hamate* (Haw.)Sweet	Euphorbiaceae
88	*Indingofera exigua* Eckl. &Zeyh.	Fabaceae
89	*Lotononis hirsute Benth.*	Fabaceae
90	*Lotononis digitatta Benth.*	Fabaceae
91	*Lotononis falcate Benth.*	Fabaceae
92	*Vigna vexillata var. ovata* (L.)A.Rich	Fabaceae
93	*Acacia karoo* Hayne	Fabaceae
94	*Prosopis glandulosa* Torr.	Fabaceae
95	*Ornithogalum suaveolens* N.J.von Jacquin	Hyacinthaceae
96	*Gladiolus saccatus* L.	Iridaceae
97	*Limeum africanum* L.	Limeaceae
98	*Hypertelis salsoloides (*Burch.)Adamson	Molluginaceae
99	*Aristida barbicolis* L.	Poaceae
100	*Enneapogon scaber* Lehm.	Poaceae
101	*Enneapogon avenaceus* (Lindl.) C.E.Hubb	Poaceae
102	*Karroochloa schismoides* (Stapf ex Conert) Conert & Turpe	Poaceae
103	*Schmdta kalahariensis* Stent.	Poaceae
104	*Stipagrostis ciliata* (Desf.)De Winter	Poaceae

105	*Stipagrostis obtusa* Delile Nees	Poaceae
106	*Stipagrostis schaeferi* (Mez)De Winter	Poaceae
107	*Ziziphus mucronata* Willd.	Rhamnaceae
108	*Thesium lineatum* Linn.f.	Santalaceae
109	*Aptosimum spinescence* (Thunb.)F.E Weber	Scrophulariaceae
110	*Hebernstretia parviflora* E.Mey.	Scrophulariaceae
111	*Jamesbrittenia filicaulis* (Benth.)Hilliard	Scrophulariaceae
112	*Jamesbrittenia grandifolia (*Galpin*)* Hilliard	Scrophulariaceae
113	*Nemasia anisocarpa* E.Mey.ex Benth	Scrophulariaceae
114	*Nemesia strumosa* (Benth.)Benth	Scrophulariaceae
115	*Nemesia karroensis* Bond.	Scrophulariaceae
116	*Nemesia caerulea* Hiern	Scrophulariaceae
117	*Nemesia violiflora* Roessler	Scrophulariaceae
118	*Peliostomum leucorrhizum* E.Mey. ex Benth	Scrophulariaceae
119	*Peliostomum virgatum* E.Mey. ex Benth	Scrophulariaceae
120	*Solanum sisymbriifolium* Lam.	Solanaceae
121	*Tamarix usneoides* E.Mey	Tamaricaceae
122	*Cyanella hyacinthoides* Royen ex L.	Tecophilaeaceae
123	*Forsskaolea hereroensis* Schinz	Urticaceae
124	*Tribulus cristatus* L.	Zygophyllaceae
125	*Tribulus pterophorus* C.Presl.	Zygophyllaceae
126	*Tribulus zeyheri* Sond.subsp.zeyheri	Zygophyllaceae