Spatio-Temporal Variation In Forage Production In A Key Resource Area In Succulent Karoo Rangeland, South Africa

Martha Konje
Kenyatta University, Department of Plant Sciences, P.O Box 43844 - 00100, Nairobi, Kenya

Paul Muoria
Kenyatta University, Department of Plant Sciences, P.O Box 43844 - 00100, Nairobi, Kenya,

Emily Wabuyele
Kenyatta University, Department of Plant Sciences, P.O Box 43844 - 00100, Nairobi, Kenya

Susanne Vetter
Department of Botany, Rhodes University, P.O. Box 94, Grahamstown, 6140, South Africa

ABSTRACT

For herbivores to survive in arid rangelands, they largely depend on landscapes that act as grazing reserves during the dry seasons. In Richtersveld National Park, the dry season forage consists of browse from tree branches, litter and grass that grow along the Orange River. The aim of the study was to determine how browse production by tree species along the riparian zone (a key resource area), vary between the sites, with time and among the tree species, as well as the implication of a dry season key resource in management of rangelands. Sampling of tree species took place at three study sites along the riparian zone. In each site, temporal available standing biomass, browse and litter production by the seven dominant tree species were sampled. To calculate the total biomass production per tree canopy area, branch-count method was used up to a height of 1.5 m. Browse production differed between the tree species and between sampling periods but not between the sampling sites. Key resource area was found to play an important role in sustaining herbivores populations during the dry seasons as well as to reduce the negative effects associated with continuous grazing on the landscapes.

Key Words: Browse, Herbivores, Pastoralism, Richtersveld, Riparian, Equilibrium

1. INTRODUCTION

Pastoralists have well adapted livestock management strategies that guide them to survive in arid ecosystems which are characterised by variation in climatic conditions and shortage of forage resource (Salomon *et al*. 2013). Herbivores that survive during the dry season in arid rangelands are largely dependent on their ability to exploit parts of the landscapes that are rich in resources. Scoones (1993) referred them as 'fertile pockets' of the landscapes and according to Illius and O'Connor (2000), they are the 'key resource areas' in arid rangelands. 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 Richtersveld National Park (RNP) in the Succulent Karoo rangeland, the riparian zones acts 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*. 2016) 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 arid and semi-arid 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). However these plants are indigenous to RNP. 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 spend their time browsing. The quality and quantity of available browse forage, time spent browsing and the influence of the farmers 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), 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 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 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 strongly to rainfall but the main water source of the riparian zone may be a river as in RNP where water source is the Orange River. The river water levels are mainly determined by the summer rainfall regions in the interior of South Africa. Orange River originates from Drakensberg in Lesotho and flows westward for 2200 km, through Richtersveld desert and finally reaches the Atlantic Ocean at Alexander Bay (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 a great role in sustaining vegetation growth 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.

Presence of a large key resource such as the Orange River riparian zone in Richterseld National Park in the Succulent Karoo is likely to influence the equilibrium between forage availability and herbivores populations in a rangeland. According to Illius and O'Connor (1999 and 2000), alternating wet and dry seasons impose a cycle of plant growth and phenology that results in forage abundance and supply needed to sustain herbivores populations in arid ecosystems. During the dry season when there is low food supply, animals migrate to the key resource area along the river and this has enabled pastoralists to sustain their herds' populations throughout the years. Spatial separation of grazing areas during the wet and dry seasons has important implications for the dynamics of herbivores population and their impact on vegetation. In arid rangelands animals 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 herbivores populations are at equilibrium with forage supply (Illius and O'Connor, 2000). 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 dry season. On the other hand, 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 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 each woody plant species to the browse production and (iii) the implication of a dry season key resource in management of 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.

2. MATERIALS AND METHODS

2.1 STUDY AREA

The Richtersveld National Park (RNP) is located in Namaqualand, north-western South Africa, (28° 15' S, 17° 10' E) shown in Figure 1. The park covers a total area of 162,445 ha and is an arid and semi-arid shrubland which is part of the Succulent Karoo and Desert Biomes of South Africa (Mucina and Rutherford 2006). The Succulent Karoo Biome is globally recognised as an arid Biodiversity Hotspot and is associated with endemism of wide range of faunal and floral groups, with Thirty per cent (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 proclaimed on 14th August 1991 (Hendricks *et al.*, 2004). Semi-nomadic pastoralism has been practised by the Nama in the Richtersveld for about 2000 years (Webley *et al.* 1993). The vegetation of the RNP is characterised by a variety of succulent's plants, woody shrubs, diverse annuals and geophytes, with dwarf succulent shrubs of the family Aizoaceae being the most distinctive family in the Succulent Karoo (Mucina *et al*. 2006). Herbivores feed on these succulents during the wet season. Trees and grasses occur mainly along the Orange River riparian zone which acts as key forage resource during the dry season.

RNP is an arid winter rainfall area, with high inter-annual rainfall variability. Mean annual rainfall varies from 102 mm in the low-lying valley of the Orange River to 52 mm and 98 mm in the desert parts in the lower lying central plains, to 248 mm in the mountainous parts of the interior. Temperatures varies between 25ºC in January and 14ºC in June and can rise to above 50ºC in the summer and drop to freezing point on winter nights. 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 stretching towards the Orange River belt.

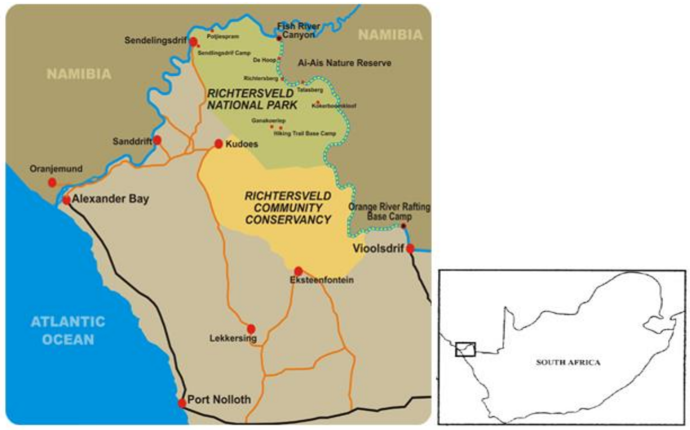


Figure 1: Map of Richtersveld National Park within the larger Succulent Karoo in South Africa (Source: Mucina and Rutherfold, 2006)

2.2 FORAGE RESOURCE PARTITIONING AND UTILIZATION IN RNP

In Richtersveld National park, pastoralists 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, with particular stock owners typically using the same set of stock posts in different years (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. There are 26 registered pastoralists whose rights to graze livestock in the park are recognised, and 270 stock posts have been established in the park over time (Figure 2). There is resource use partitioning in the RNP with different landforms being utilized at different times of the year. During the cold wet season (May-August) animals utilize forage in the mountains and plains throughout the park, while in the dry summer period (September - April) they move to the riparian zone of the Orange River due to availability of browse and water (Hendricks *et al*. 2004). The flocks of livestock consist primarily of Boer goats and some sheep.

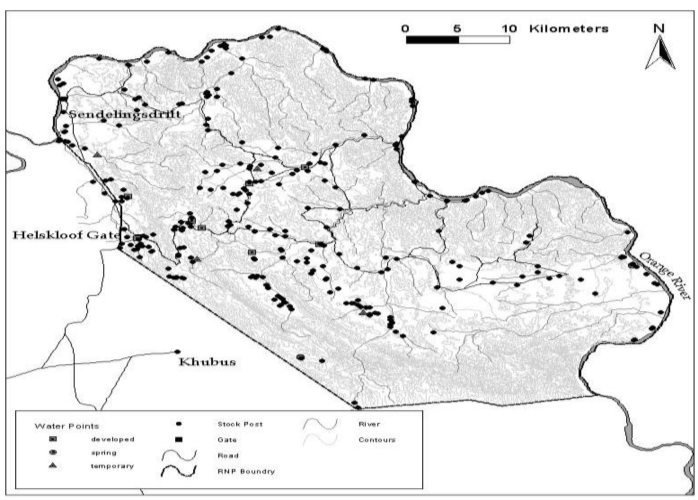


Figure 2: Distribution of stock posts (black dots) in Richtersveld National Park

(Source: Hendricks et al. 2004)

2.3 DATA COLLECTION IN THE RIPARIAN ZONE

Sampling took place at three study sites in the Orange River riparian zone namely Potjiespram, DeHoop and Richtersberg. In each site, 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 during the dry season.

2.3.1 MEASUREMENT OF VARIATION IN AVAILABLE STANDING BIOMASS

The browse available to goats was measured from October to April - the period when the herbivores move to the riparian zone to feed on browse from trees and grasses along the river. 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 (Rosenschein *et al*. 1999) that 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. Before harvesting was done branch length and diameter were measured. 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 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. Counting and harvesting of branches were done after every two months (in September 2006, November 2006, January 2007 and April2007, 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.

2.3.2 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. In order to determine the ecological factors that influence trees browse production in RNP, the Best Model Selection was used with an assumption that there were more than one ecological factors that would determine browse production. The Best Model Selection was done to determine whether browse production in RNP was influenced by rainfall or river water levels. In this model winter rainfall between June (onset of winter rainfall) and sampling months was considered as R1 while the annual rainfall of the sampling year was considered as R2. River water level of the sampling month was considered as RW2, water levels of the previous month as RW1 and cumulative river water level of the two months as RW3.

2.3.3 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. 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.

2.3.4 MEASUREMENT OF GRASS BIOMASS PRODUCTION

Grass in RNP was found in patches along the Orange River banks. Grass cover stretch along the riparian zone. To measure grass biomass production, transects of I km long parallel to the river were measured at each site. Plots of 1 m x 1 m plots were laid, and grass was harvested. Mobile cages of 1 m x 1 m 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 were 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.

2.3.5 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 recorded at a station within RNP 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 (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.

2.3.6 RAINFALL DATA

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

2.4 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. 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 test the difference between the amount of litter produced per tree species as well as the contribution of leaves, fruits, flowers and twigs to the total litter production. ANOVA was used to test for the effect of sites, sampling period and species at significance level of 95 percent confidence intervals of available browse, litter and browse production.

3. RESULTS

3.1 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 1. Regression equation between browse biomass and stem diameter showed that *Euclea pseudebenus* had the highest R^2 value of 0.79 followed by *Rhus pendulina* 0.78, *Prosopis glandulosa* 0.74 and *Maytenus linearis*. 0.74. *Tamarix usneoides* had the lowest R^2 value of 0.61. Regression equation between available browse biomass and branch length show that *Ziziphus mucronata* had the highest R^2 value of 0.80, followed by *Acacia karoo* 0.74, Rhus *pendulina* 0.73 and *Prosopis glandulosa* 0.72. *Tamarix usneoides* had the lowest R^2 value of 0.62 (Table 1). The regression equations of different tree species were used to calculate the total available browse production of each species at a height of 1.5 meters (the height at which forage is available to goats).

Table 1: Regression equations between total available browse biomass and branch dimensions for each tree species

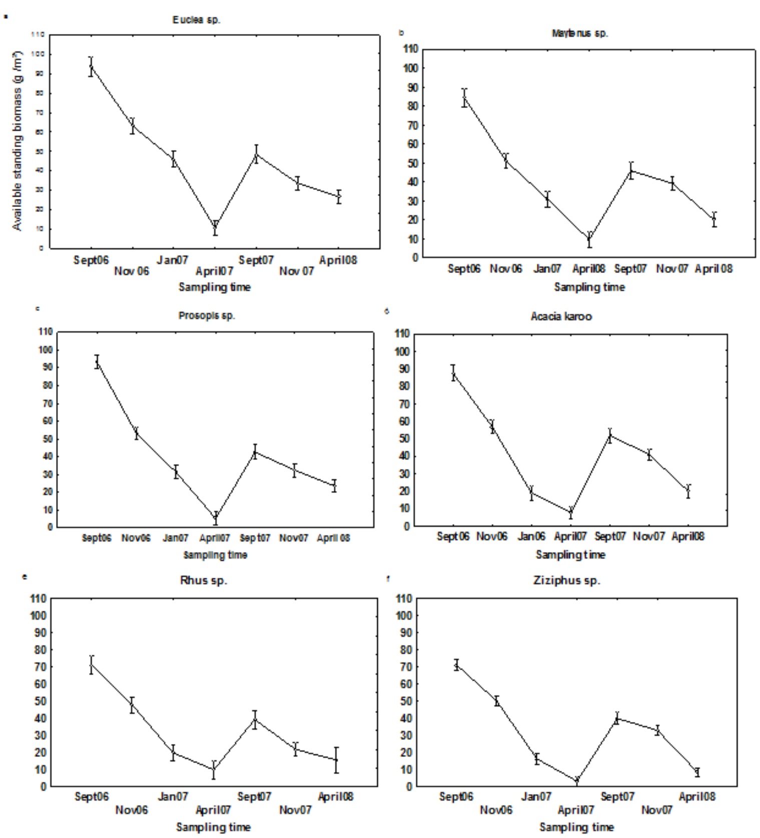
Species	Branch diameter vs biomass		Branch length vs biomass	
	R^2	Equations	R^2	Equations
A. karoo	0.66	y = 2.696x + 20.34	0.74	y = 31.36x + 13.82
E. pseudebenus	0.79	y = 3.292x + 22.28	0.71	y = 34.25x + 22.84
M. linearis	0.74	y = 3.271x + 16.39	0.67	y = 31.31x + 19.51
P. glandulosa	0.74	y = 3.184x + 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

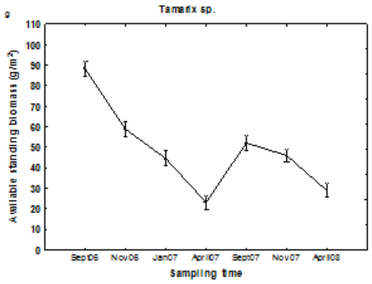
Abbreviated species are: Acacia karoo, Euclea pseudebenus, Maytenus linearis, Prosopis glandulosa, Rhus pendulina, Tamarix usneoides and Ziziphus mucronata

3.2 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 all tree species (Figure 3a-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. *Euclea pseudebenus* and *Prosopis glandulosa* had the highest available standing biomass at the beginning of summer periods before any browsing had taken place (Figure 3a-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 *Ziziphus mucronata*, *Rhus pendulina*, *Acacia karoo*, *Prosopis glandulosa*, *Euclea pseudebenus*, *Maytenus linearis* and *Tamarix usneoides respectively* (Figure3a-g).

Available standing biomass differed significantly between the species ($p<0.05$; $F_{(5, 676)}=69.383$) and between sampling season ($p<0.05$; $F_{(5, 676)}=1299.7$) but did not differ significantly between sites ($p>0.05$; $F_{(1, 676)}=0.00456$) as shown in Table 2. There was a significant interaction between sampling time and different tree species, sampling time with sites but there was no significant interaction between sites and species (Table 2). Results show that browse production differed significantly between the species and between sampling season but did not differ significantly between sites.





(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 3a-g: Temporal variation in available browse during summer period from September 2006 to April 2008 of the seven tree species. Vertical bars denote 0.95 confidence intervals.

Table 2: Level of significance in available standing biomass for the period September 2006 to April 2008

Effects	P-value	F-value
Species	<0.001	$F_{(5, 676)}$=69.383
Sampling time	<0.001	$F_{(5, 676)}$=1299.7
Sampling time*Species	<0.001	$F_{(35, 676)}$=7.4105
Sites	>0.05	$F_{(1, 676)}$=.00456
Sites * Species	<0.05	$F_{(11, 676)}$=2.3546
Sampling time*Sites	>0.05	$F_{(11, 676)}$=.56430

3.3 MEASUREMENT OF SPATIAL AND TEMPORAL BROWSE PRODUCTION

Browse production here refers to forage produced by tree species after every two months (between November 2006 and April 2008). Results presented in Table 3 show that browse production was significantly different between the 7 tree species ($p<0.05$; $F_{(6, 84)}$ =5.614), in different sampling time ($p<0.05$; $F_{(5, 84)}$=11.137) and between the three study sites ($p<0.05$; $F_{(2, 105)}$=3.432). Browse production also was significantly different between the two years 2006 and 2007 ($p<0.05$; $F_{(1, 112)}$=5.356). There was a significant effect between browse production in different study sites and species ($p<0.05$; $F_{(12, 105)}$=3.101), sampling time with species ($p<0.05$; $F_{(30, 84)}$=0.4875) but there was no significant interaction of sampling time with sites as well as years with species (Table 3)

Table 3: Variation in browse production between September 2006 and April 2008

**denote significant difference at $P \leq 0.05$*

Interactions	P-value	F-value
Species	<0.001*	$F_{(6, 84)}$=5.61
Sampling time	<0.001*	$F_{(5, 84)}$=11.13
Sites	<0.05*	$F_{(2, 105)}$=3.43
Sites verses Species	<0.001*	$F_{(12, 105)}$=3.11
Sampling time verses Species	<0.05*	$F_{(30, 84)}$=0.487
Sampling time verses Sites	>0.05	$F_{(10, 108)}$=0.65
Study years	<0.05*	$F_{(1, 112)}$=5.36
Study years verses Species	>0.05	$F_{(6, 112)}$=0.35

There was significant difference between browse production in the 3 study sites (p<0.005; F (12, 105) = 3.10) as shown in Figure 6.5. Browse production by *Acacia karoo, Rhus pendulina, Euclea pseudebenus* and *Ziziphus mucronata* was significantly different between the 3 study sites (Figure 4). Browse production by *Prosopis glandulosa* was significantly lower in Richtersberg but there was no significant difference in browse production between Poijispram and DeHoop sites. Browse production by *Tamarix usneoides* was significantly higher in Richtersberg but was not significant different between the other two study sites. Browse production by *Maytenus linearis* was significantly higher in DeHoop but was not significant different between Poikiespram and Richtersberg (Figure 4).

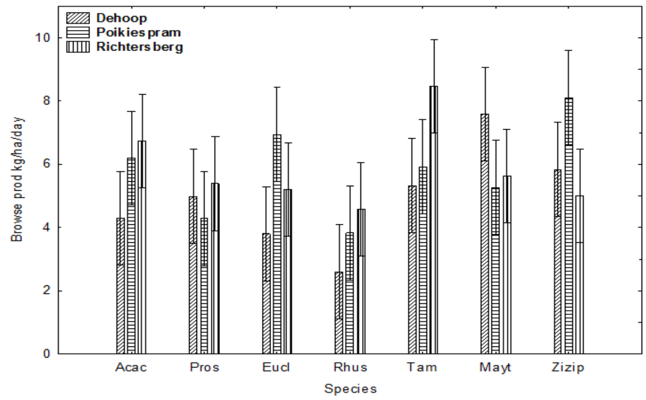


Figure 4: Variation in browse production between the 3 study sites

(Abbreviated trees species are: Acacia karoo, Prosopis glandulosa, Euclea pseudebenus, Rhus pendulina, Tamarix usneoides Maytenus linearis, and Ziziphus mucronata)

3.4 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<0.001; $F_{(6, 13)}$=69.87) and between sampling time (p<0.001; $F_{(5, 85)}$=4.68) but did not vary between sites (Table 4). There was significant difference in browse production by different species with sampling time (p<0.001; $F_{(30, 65)}$=5.96) but there was no significant interaction between study sites and sampling time (Table 4). Litter production by *Acacia karoo* was significantly higher than the other tree species (Figure 5). *Rhus pendulina* produced the lowest amount of litter compared to the other tree species. However there was no significant difference in litter production by *Prosopis glandulosa, Ziziphus mucronata,* and *Euclea pseudebenus* tree species although it was higher than the litter produced by *Maytenus linearis* and *Tamarix usneoides* species (Figure 5). Litter production differed significantly between sampling time (Figure 6) 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 and 7). Abbreviated tree species are *Acacia karoo, Prosopis glandulosa Euclea pseudebenus, Rhus pendulina, Tamarix usneoides Maytenus linearis,* and *Ziziphus mucronata.*

Table 4: Litter production between species, sites and sampling time

Effect	P-value	F-value
Species	<0.001	$F_{(6, 13)}$=69.87
Sites	>0.05	$F_{(2, 17)}$=0.42
Time (Sampling time)	<0.001	$F_{(5, 85)}$=4.68
Species* Time	<0.001	$F_{(30, 65)}$=5.96
Sites * Time	>0.05	$F_{(10, 85)}$=0.74

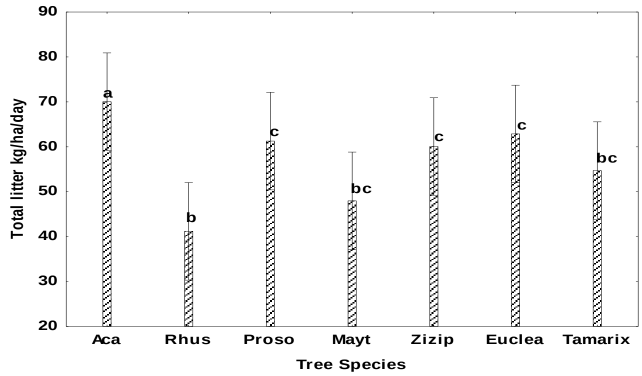


Figure 5: Total litter production by different species. Different letter shows significant difference while same letter shows no significance difference. Vertical bars denote 0.95 confidence intervals.

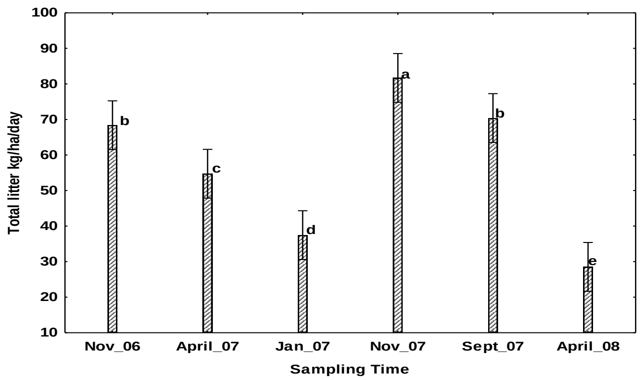


Figure 6: Temporal variation in total litter production (November 2006 to April 2008). Different letter shows significant difference while same letter shows no significance difference. Vertical bars denote 0.95 confidence intervals.

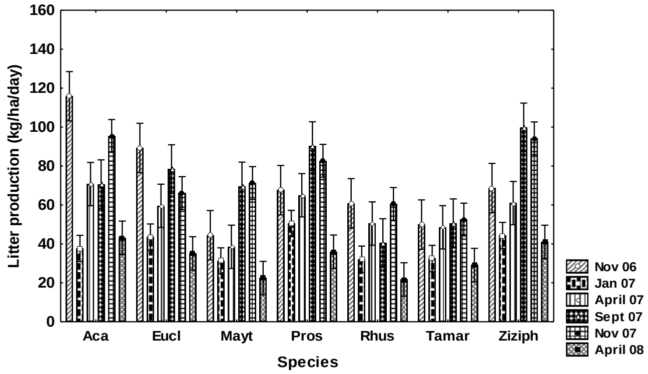


Figure 7: Litter produced by different species at different sampling times of the year.

Abbreviated tree species are - (Acacia karoo, Prosopis glandulosa Euclea pseudebenus, Rhus pendulina, Tamarix usneoides Maytenus linearis, and Ziziphus mucronata)

Leaves contributed the highest percentage of litter component followed by twigs while fruits and flowers contributed lower percentage. Leaves of *Tamarix usneoides* 59.8%, *Prosopis glandulosa* 55%, and *Maytenus linearis* 54.9% species had the highest percentage contribution to the total amount of litter. *Euclea pseudebenus*, *Ziziphus mucronata* and *Prosopis glandulosa* species contributed the highest amount of fruits in the litter respectively. *Acacia karoo*, *Euclea pseudebenus*, and *Rhus pendulina* species produced the highest amount of flowers respectively while *Tamarix usneoides*, *Maytenus linearis*, *Acacia karoo* and *Euclea pseudebenus* produced the highest amount of twigs component of the litter. 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 8).

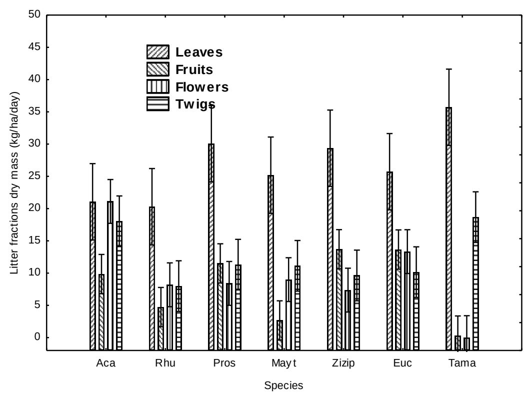


Figure 8: Contribution of different litter components from different tree species to the total litter production (November 2006 to April 2008). Vertical bars denote 0.95 confidence intervals.

(Abbreviated tree species - Acacia karoo, Rhus pendulina Prosopis glandulosa, Maytenus linearis Ziziphus mucronata, Euclea pseudebenus, and Tamarix 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 *Acacia Karoo* was significantly higher than the other tree species. *Rhus pendulina* produced the lowest amount of litter compared to the other tree species. However there was no significant difference in litter produced by *Prosopis glandulosa*, *Ziziphus mucronata*, and *Euclea pseudebenus* tree species although it was higher than the litter produced by *Maytenus linearis* and *Tamarix 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.

3.5 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). Interaction between grass biomass and river water levels as well as interaction between grass biomass production and rainfall had positive correlation at P<0.0001 as shown in Figure 6.

Table 6: Influence of river water levels and rainfall on grass biomass production and availability

** Denotes significant differences at P ≤ 0.05*

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	**0.0001***
Sampling period	1	5.60	0.021
Grass Biomass vs time	1	3.32	0.073
Rainfall	1	2.30	0.127
Grass Biomass vs rainfall	1	629.40	**0.001***
Sampling sites	1	0.04	0.83
Grass Biomass vs sites	1	0.31	0.58

River water levels were found to be low in the months of September in 2006 and in April in 2007 and 2008. On the other hand, river water levels were higher in the months of November in 2006 and January and November in 2007. 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.. River water levels were found to have a significant influence on grass forage production and availability as shown in Table 6. 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.

4. DISCUSSION

4.1 SPATIAL AND TEMPORAL BROWSE PRODUCTION

One of the major constraints to livestock production in arid and semi-arid rangelands is spatial and temporal variation in availability of forage (Olafadehan and Adewumi, 2009). Because of rainfall variation, coupled with diverse landscapes in arid rangelands, there is usually no guarantee of forage availability throughout the year. Browse from trees and riparian zones therefore serves a key role as the main source of forage during the dry summer season in Richtersveld National Park (Hendricks *et al*. 2005b; Hempson, *et al*. 2015). The advantage of browse as forage for herbivores especially during the dry season is the ability to retain green leaves and litter especially during dry seasons when herbaceous plant and legumes dry up due to long periods of high temperatures without rainfall (Olafadehan and Okunade, 2018).

Browse from trees along the riparian zone in RNP were found to bridge the gap of forage availability during the dry seasons. In addition browse from woody trees have also been found to be good source of protein and energy for ungulates (Olafadehan, 2013; Otieno *et al*. 2019). 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 regression between stem length and diameter with available standing browse (R^2 of 0.61 to 0.8). Allometric models have been used in other studies to assess browse production (Baumert and Khamzina, 2015; van der Vyver and Cowling 2019) and they were found to be 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, Rhus pendulina*, *Acacia karoo, Prosopis glandulosa* were found to contribute to forage and were more preferred by herbivores while *Euclea pseudebenus, Tamarix usneoides* and *Maytenus 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 *Ziziphus mucronata, Rhus pendulina, Acacia karoo, Prosopis glandulosa* respectively while on the other hand, minimal reduction in available browse was recorded in *Euclea pseudebenus*, *Tamarix usneoides* and *Maytenus 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 *Ziziphus mucronata*, *Rhus pendulina* and *Acacia karoo* with increase in adult goat density, and *Ziziphus mucronata* and *Rhus pendulina* being the most preferred browse species in RNP.

It was clearly evident that not all forage available in the study sites was of benefit to the herbivores in RNP. Although *Ziziphus mucronata*, *Rhus pendulina, Acacia karoo*, and *Prosopis glandulosa* were the most preferred species for browsing by goats, on the other hand it was *Euclea pseudebenus, Tamarix usneoides* and *Prosopis glandulosa* that had the highest browse production. In RNP goats were found to avoid feeding on the browse of *Euclea pseudebenus*, *Tamarix usneoides* and *Maytenus linearis* despite the fact that the three species do not have morphological deterrents such as thorns. Studies have shown that leaves of some woody species are usually associated with high concentration of secondary metabolites (Otieno *et al*. 2019) and thus not consumed by animals. For *Prosopis. glandulosa* species 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 *Prosopis. glandulosa* have been documented as nutritious food source for wildlife and livestock.

Ziziphus 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). *Ziziphus mucronata* was followed by *Rhus pendulina, Acacia karoo and Prosopis 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 thorny-less species that were tannin-rich. In this study woody species that were browsed more such as *Ziziphus macronata*, *Acacia karoo* and *Prosopis glandulosa* have thorns (except *Rhus pendulina*) while woody species that were not preferred for browsing (*Euclea pseudebenus*, *Tamarix usneoides* and *Maytenus linearis)* had no thorns.

Another observation was that there was no significant difference between the total browse production in the three 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 seven woody species, *Acacia karoo* contributed the highest amount of litter. Depending on browse preference for each species, the study therefore shows that fruits from *Ziziphus mucronata* and *Prosopis grandulosa* contributed the highest amount of palatable litter, followed by flowers of *Acacia karoo* and *Rhus pendulina* This may be attributed to the earlier observations in the depletion of available browse on branches of the seven species, that herbivores in RNP had less preference for browse from thornyless species such as *Euclea pseudebenus, Tamarix usneoides*, and *Maytenus 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 arid rangelands such as RNP.

4.2 GRASS FORAGE PRODUCTION IN THE RIPARIAN ZONE IN RNP

Orange River water levels had influence on availability and accessibility of grass forage to herbivores in RNP unlike the rainfall. This was mainly because the sources of the Orange River water was far beyond the boundaries of RNP and could not be attributed to the rainfall that was recorded in RNP during the period of the study. River water levels were found to have a significant influence on grass forage production and availability.

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 (Figure 9). 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. 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. 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.

4.3 IMPLICATION OF A DRY SEASON KEY RESOURCE IN MANAGEMENT OF ARID RANGELANDS

The key resource model of Illius and O'Connor (1999 and 2000) predict that animal numbers are regulated in a density- dependent manner by the limited forage available for use in the dry season, with the numbers being virtually uncoupled from resource elsewhere in the system. The model stresses that the presence of a key resource (dry season ranges) mostly in areas along perennial rivers or artificial water points enables heavier use of wet season ranges than if this key resource were absent. A consequence of this is that animal numbers and range production tend to become uncoupled especially during drought and this carries the risk of ecological change, reduced forage productivity and flow of goods and services to pastoralists (Illius and O'Connor, 2000). Samuels *et al.* (2013) concluded that in arid rangelands, landscape heterogeneity plays a big role in the conservation of the ecosystem by reducing the likelihood of grazing induced degradation and enhancing productivity. During the dry season resource limitation occurs, low food quality and quantity causes animals to lose weight and their survival depends on the body fat reserves carried over from the growing season (Hendricks *et al*. 2005b).

Alternating wet and dry season's resource use imposes a cycle of plant growth and phenology resulting into food abundance and quality (Samuels *et al* 2013). Spatial separation of range areas accessible during the wet and dry seasons is therefore regarded as having important implication for the dynamics of herbivore populations and their impact on vegetation. Herbivore populations would be expected to be slightly stable under spatial resource utilization than would be the case if all resources were accessible throughout the year (Illius and O'Connor 2000). Spatial variability and accessibility of resources buffer seasonal variability of animal populations by allowing a dry-season refuge to herbivores (Samuels *et al*, 2019). Much of developing nations lack policies that are directed toward balancing of the conservation and management of rangeland resources and the wellbeing of pastoral communities that depend on them. Dry season resource areas are of considerable value due to their unique rich biodiversity and their role in sustaining herbivores populations and pastoralists livelihoods especially during the dry seasons. Therefore, loss of access to dry season resource areas has far reaching implications for the viability of pastoralism and rangeland ecosystems.

4.4 CONCLUSIONS AND RECOMMENDATIONS

The key resource theory, which is supported by Hempson *et al*. 2015, states that bigger key resources are likely to lead to more impact on the wet season resources as they allow bigger populations to be maintained which then exert grater grazing pressure on the wet season resource in the wet season. A prolonged dry season has been found to result into an equilibrium state in the key resource area since depletion of resources is likely to occur. Extreme climate variability lead to decoupling of herbivores numbers and the forage resource during the dry season as browsed was completely depleted with time. This would eventually result into decline in population sizes of herbivores, poor body conditions, low yields and death of animals in an equilibrium and density- dependent manner. In RNP depletion of browse from trees in riparian belt during the dry season was associated with height effect from bottom up to a height of 1.5m and as animal population increased forage depletion occurred in a density-dependent manner (Hempson *et al*., 2015). Understanding spatial-temporal variation in forage production and utilization in RNP, how the available browse forage vary with time in different landscapes and the contribution of a key resource area in the pastoral systems will be of great importance in the management of this arid ecosystem.

Management policies in such an arid ecosystems should embrace the complexity of the spatial and temporal heterogeneity that exists in arid rangelands. This can reduce the effect of climate variability on herbivores and on rangeland conditions. Further studies should be conducted on the nutritive value of browse forage from different woody plants available in the riparian zone in RNP which serve as supplements of forage during the dry season to confirm the reasons why there was variance in their preference by herbivores. 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 arid rangelands globally. It is important for park management to handle potential conflicts that are likely to occur between pastoralists and tourists along the riparian zone in RNP. Tourism and camping sites along the river in RNP can be a big negative effect on goat populations and livelihood of pastoralists if were excluded from these areas. Conflicts between local communities, governments and private developers have been reported globally in most arid rangelands, mainly due to lack of policies directed toward balancing the wellbeing of rural pastoralists, economic activities such as crops farming, mining and tourism and conservation of rangeland resources. 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.

ACKNOWLEDGEMENTS

I acknowledge the field assistants, staff and the pastoralists of Richtersveld National Park for the information and support. I appreciate the financial support from South Africa National Research Fund through Rhodes University to carry out the research.

5. REFERENCES

Baumert, S., Khamzina, A. (2015). Allometric relations in Jatropha curcas production systems of Burkina Faso. *Journal of Arid Environments*, 120:95-104

Ganqa, N. M, Scogings, P. (2007). Forage quality, twig diameter, and growth habit of woody plants browsed by black rhinoceros in semi-arid subtropical thicket, South Africa. Journal of Arid Environments, 70, 514-526

Gillan, F. K, McClaran, M. P., Swetnam, T. L., & Heilman, P. (2019). Estimating Forage Utilization with Drone Based Photogrammetric Point Clouds. Rangeland Ecology and Management, 72,575-585

Hempson G. P, Illius, A. W., Hendricks, H. H, Bond, W. J., & Vetter, S. (2015). Herbivore population regulation and resource heterogeneity in a stochastic environment, *Ecology*, 96(8), 2170–2180

Hendricks, H. H., Midgley, J. J., Bond, W. J., Novellie, P. A. (2004). Why communal pastoralists do what they do in the Richtersveld National Park. *African Journal of Range and Forage Science*, 21, 29-36

Hendricks, H. H., Clark, B., Bond, W. J., Midgley, J. J., & Novellie, P. A. (2005b). Movement response patterns of livestock to rainfall variability in Richtersveld National Park. *African Journal of Range and Forage Science* 22 (2), 117-125

Illius, A., O'Connor, T. (1999). On the relevance of non-equilibrium concepts to semi-arid grazing systems. *Ecological Applications*, 9, 798-813

Illius, A., & O'Connor T. (2000). Resource heterogeneity and ungulate population dynamics. *Oikos*, 89

Leparmarai, P. T., Mwangi, D. M., Gluecks, I., Mutie, F. M., & Marquardt, S. (2018). Plant selection and performance of two cattle types and camels on semi-arid rangelands in Kenya. *Rangeland Ecology and management*, 71 (6), 798-806

Mucina, L., & Rutherfold M. C. (2006). *The vegetation of South Africa, Lesotho and Swaziland, Pretoria, South Africa*. 220- 299

Mucina, L., Jurgens, N., Le Roux A., Rutherfold, M. C., Schmiedel, U., Esler, K. J., Powrie, L. W., Desmet, P. G., & Milton, S. J. (2006). *Succulent Karoo Biome*. **In**: Mucina, L. & Rutherfold, M. C (Editors). *The vegetation of South Africa, Lesotho and Swaziland, Pretoria, South Africa*, PP 220- 299

Mukeka, J. M., Ogutu, J. O., Kanga, E., & Roskaft, E. (2019). Human Wildlife conflicts and their correlates in Narok County, Kenya. *Global Ecology and Conservation*, 18, 1-22

Müller, J. L., Babu, M. M., Saklani, P. L., Mayer, A. C., & Kreuzer, M. (2012). Forage resource use by cattle or goats at an Indian protected area: Differences and implications for conservation. *Journal of Arid Environments*, 77, 130-137

Naah, J. S. N., & Guuroh, R. G. (2017). Factors influencing local ecological knowledge of forage resources; Ethnobotanical evidence from West Africa's savannas. *Journal of Environmental Management*, 188, 297-307

Olafadehan, O. A., & Okunade, S. A. (2018). Fodder value of three browse forage species for growing goats. *Journal of the Saudi Society of Agricultural Sciences*, 17, 43-50

Olafadehan, O. A., & Adewumi, M. K. (2009). Productive and reproductive performance of strategically supplemented free grazing prepartum Bunaji cows in agropastoral farming system. *Trop. Anim. Health Prod*., 41, 1275-1281

Otieno, T. O., Gohen, J. R., Webala, P. W., Mwangi, A., & Ford, A. T. (2019). Human and Risk mediated browsing pressure by sympatric antelope in an African Savanna, *Biological Conservation*, 232, 59-65

Saayman, N., Morris, C., & Botha, H. (2016). Livestock grazing has minimal effect on the species richness and diversity of semi-arid shrubland in the western little Karoo South Africa. *African Journal of Range and Forage Sciences*, 26, 169-179

Salomon, M., Cupido, C., & Samuels, M. I. (2013). The good shepherd: remedying the fencing syndrome. *African Journal of Range and Forage Science* 30(1), 43-54

Samuels, M. I., Allsopp, N., & Hoffman, M. T. (2019). Traditional mobile pastoralism in a contemporary semi-arid rangeland in Namaqualand, South Africa. *Rangeland Ecology and Management,* 72(10), 195-203

Samuels, M. I., Allsopp, N., & Hoffman, M. T. (2013). How could herd mobility be used to manage resources and livestock grazing in semi-arid rangeland commons? *African Journal of Range and Forage Science,* 30(1&2), 85-89

Scoone, I. (1993). Why are there so many animals? Cattle population dynamics in the communal areas of Zimbambwe In: Behnke, R.H and Scoones, I, Kerven, C. (Eds). Range Ecology at Disequilibrium: New Model of Natural Variability and Pastoral Adaptations in Africa Savanna. Overseas Development Institute, London. Pp 248

Skarpe, C., Jannson, I., Seljeli, L., Bergstrom, R., & Roskafit, E. (2007). Browsing by goats on three spatial scales in a semi-arid savanna. *Journal of Arid Environment,* 68 (3), 480- 491

Tolleson, D. R., Rhodes, E. R., Malambo, L., Angerer, J. P., & Popescu, S. C. (2019). Old School and High Tech: A comparison of methods to quantify ash juniper biomass as fuel or forage. *Rangelands*, 41(4), 159-168

van der Vyver, M. L, & Cowling, R. M. (2019). Aboveground biomass and carbon pool estimates of above ground biomass and carbon pool estimates of Portulacaria afra (spekboom)-rich subtropical thicket with species-specific allometric models. *Forest Ecology and Management*, 448, 11-21

Vetter, S. (2005). Rangelands at equilibrium and non-equilibrium: Recent developments in the debate. *Journal of arid environment*, 62, 321-341

Webley, L., Archer, F., & Brink, J. (1993). Die Toon: a late holocene site in the Richtersveld National Park, northern Cape. *Koedoe* 36(2), 1 – 9

Williamson, G. (2000a). Notes on the vegetation and climate of the Richtersveld National Park. *Aloe*, 31 (4), 83 - 87

Exclusive Journal publishing house