Using nutritional quality of forage and faeces for predicting sustainable livestock and game stocking rates at Pniel Estates in Northern Cape, South Africa

Khanyisile R. Mbatha

Dissertation presented for the degree of

Philosophy of Doctorate

at the

University of Stellenbosch

Promoter: Prof. David Ward

Co-promoter: Dr W. Scotney Watts

April 2006

Declaration

I, the undersigned, hereby declare that the work contained in this dissertation is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

……………………..

Khanyisile R. Mbatha

April 2006

Abstract

The aim of the study was to assess the importance of spatial and temporal variation in diet quality and abundance for determining sustainable stocking rates on commercial, communal and game ranches in a semi-arid savanna, with the ultimate goal of avoiding land degradation in the long term, to provide sustainable livelihoods in rangelands and to make policy that will help in managing the available natural resources in the rangelands. Thus, firstly the effects of grazing, fire, nitrogen and water availability on nutritional quality of grass in semi-arid savanna was assessed. Secondly, spatial and temporal variation in plant quantity and quality among management (commercial, communal and game) types and habitat types (open savanna, rocky, shrubby and pans) and stocking rates in different management types were determined. Thirdly, the quality and quantity of variation inside and outside herbivore exclosures among commercial, communal and game management and habitat types in the semi arid savanna were estimated. Fourthly, faecal profiling was used to assess the effects of different management types on diet quality in semi-arid savanna. Lastly, policy based on the results of the present study was formulated.

In this semi-arid system, fire interacted with nitrogen and grazing to improve grass quality. Grazing alone had little effect on grass quality, although in the late wet season, crude protein (CP) and phosphorus (P) levels were high on grazed plots. Nitrogen addition was important because it improved grass quality, but only during the wet season, probably because of uptake limitation in the dry season.

It has been observed from the present study that the game ranch, with a wide variety of animal species had low bush encroachment, few poisonous and unpalatable plant species and high plant quality. In contrast, the commercial management type, ranching cattle only, showed the lowest dietary quality of parameters measured, had the highest signs of bush encroachment, and many poisonous and unpalatable plant species (but less than in the communal ranch), all indicating land degradation in spite of rotational grazing and lower stocking density than on the communal ranch. Our recommendation for the commercially-managed area would be to introduce a greater variety of stock and/or game to reduce selective grazing of certain plant species. We recommend that a conservative approach to stocking density be adopted by ranchers. We recognise that this strategy may result in an excess of forage in the wet season. This can be remedied by leasing land to stockowners with limited rangeland available.

The most surprising finding was that faecal quality was lowest in the commercial management type. We ascribe this to the higher nutrient deposition under communal management (due to higher stocking densities), thereby increasing soil quality, which affects plant quality in turn. An additional factor that may affect this result is that animals in the communally-managed area have freedom of movement and may be better able to access high quality food items. We may interpret this to mean that a continuous grazing system may hold some advantages over a rotational system under these circumstances. The high faecal quality of animals in the clay pan habitat with high soil nutrients shows that the pan habitat can be considered a key resource. Assessing plant species availability is not a particularly reliable method for assessing either habitat suitability or stocking rates. We recommend that faecal profiling, which explicitly incorporates diet selectivity, may be a more reliable method of managing these habitats.

The negative effects of grazing were more evident in the commercial ranch. In a rotational grazing system, these effects are probably due to returning herds to camps before the plants have had time to recover and, perhaps, due to the use of a single species of livestock, which increases the negative impacts of selective grazing. This problem may be more acute in areas such as this with low and erratic rainfall, which makes it difficult for ranchers to consistently follow a regular rotation of animals among camps. Clearly, ranchers need to follow a more flexible system of rotation and need to examine the state of the sward, moving animals into new camps only once they have recovered sufficiently from the previous period of grazing. It is evident from our study that exclosures are very useful tools for examining the effects of grazing on plant quality and composition. Policy formulation based on scientific results may be a better option for rangelands.

Keywords: faecal profiling, crude protein, phosphorus, grazing, stocking rate, plant quantity, plant quantity, management types, habitat types

Opsomming

Voorspelling van volhoubare vee- en wilddrakrag met behulp van voedingswaarde van voer en fesies by Pniel Landgoed, Noord-Kaap, Suid-Afrika

Die doel van hierdie studie was om die belang van ruimtelike en tydelike afwisseling in die kwaliteit en verspreiding van voeding te ondersoek om die volhoubare drakrag op kommersiële, gemeenskaps- en wild-plase in 'n semiwoestynagtige grasveld te bepaal. Die uiteindelike doelpunte wat gestel is was langtermyn van aard: die voorkoming van 'n daling in die kwaliteit van grond, om in volhoubare lewensonderhoud te voorsien en om beleid op te stel wat sal help met die bestuur van die beskikbare natuurlike bronne in hierdie areas. Daar moes dus eerstens vasgestel word watter gevolge weiding, veldbrande, stikstof en die beskikbaarheid van water het op die voedingswaarde van gras in 'n semiwoestynagtige grasveld. In die tweede plek is die ruimtelike en tydelike verskille in die hoeveelheid plante en die kwaliteit van bestuursvorme, habitatsoorte en konserwatiewe drakrag in verskillende bestuursvorme (kommersieël, gemeenskaps- en wild-plase) ondersoek. Derdens is die kwalitatiewe en kwantitatiewe verskille binne en buite herbivoorafskortings in kommersiële, gemeenskaps- en wild-plaas bestuurs- en habitatsoorte in semiwoestynagtige grasveld vasgestel. In die vierde plek is fekale profiele geneem om die gevolge van verskillende bestuurstyle op die kwaliteit van voeding te bepaal. As laaste onderdeel van hierdie studie is beleid, gebaseer op die resultate van genoemde ondersoek, opgestel.

Daar is bevind dat veldbrande in hierdie semi-woestynagtige ekosisteem die voedingswaarde van gras verbeter wanneer dit met stikstof in aanraking kom. Weiding alleen het nie 'n groot uitwerking op die voedingswaarde van gras gehad nie alhoewel daar in die laat reënseisoen 'n verhoging was in die vlakke van ru-proteïne (RP) en fosfor (P) in die gras in gebiede waar weiding plaasvind. Die toevoeging van stikstof – slegs tydens die reënseisoen – was belangrik, waarskynlik as gevolg van die beperkte opname daarvan in die droë seisoen.

Ondersoek wat tydends hierdie studie verrig is het verder aangetoon dat daar op wildplase met 'n wye verskeidenheid van diersoorte min indringer-, giftige en oneetbare plante aanwesig is en dat hulle eerder oor plante met 'n hoë voedingswaarde beskik. In teenstelling hiermee het kommersiële instellings waar slegs vee wei die laagste voedingswaardes by plante gemeet en die grootste aantal indringerplante asook 'n verskeidenheid van giftige en oneetbare plantspesies (alhoewel dit minder was as by gemeenskapsplase) gehuisves. Dit het gedui op die agteruitgang van grond ten spyte van roterende weiding en 'n laer drakrag as die gemeenskapsweidingsareas.

Ons sou hierdie instellings daarom aanbeveel om 'n groter verskeidenheid van vee en/of wild aan te hou om selektiewe weiding van sekere plantsoorte te voorkom. Ons sou ook die bestuurders van hierdie instellings aanbeveel om drakrag op 'n meer konserwatiewe manier te benader. Ons is bewus daarvan dat hierdie strategie tot 'n oorvloed aan weiding in die reënseisoen kan lei, maar dit kan verhelp word deur dié gebiede aan veeboere te verhuur wat slegs oor 'n beperkte aantal weidingsareas beskik.

Die mees verrassende ontdekking wat in hierdie studie gemaak is, was dat die kwaliteit van fesies die laagste was in kommersiëlie bestuurstipes. Dit kan toegeskryf word aan die hoër afsetting van plantvoedingstowwe by gemeenskapsbestuurstyle (as gevolg van die hoër drakrag) wat op sy beurt die

grondkwaliteit verhoog en dus ‘n uitwerking het op die gehalte van plante. ‘n Bykomende faktor wat ‘n gevolg kon hê op hierdie uitslag is die feit dat diere in areas wat gemeenskaplik bestuur word oor bewegingsvryheid beskik en sodoende beter toegang het tot weiding van hoë gehalte. Volgens ons interpretasie kan dit beteken dat ‘n deurlopende weidingsisteem meer voordele kan inhou onder hierdie omstandighede as ‘n rotasiesisteem. Die hoë fekale gehalte van diere in ‘n klei-agtige habitat met hoë grondvoedingstowwe bewys ook dat hierdie habitat as ‘n hoof-natuurlike hulpbron beskou kan word. Om slegs die beskikbaarheid van plantspesies in te skat is egter nie ‘n betroubare metode om vas te stel of ‘n habitat geskik is of wat die drakrag van die habitat is nie. Ons beveel daarom aan dat fekale profiele as die meer betroubare metode gebruik word om hierdie habitatte te bestuur aangesien dit duidelik rekening hou met dieetselektiwiteit.

Die nadelige uitwerking van weiding was meer voor die hand liggend by kommersiële bestuurstyle. Waar ‘n roterende weidingsisteem gevolg word, kan dit waarskynlik toegeskryf word aan veekuddes wat in kampe teruggeplaas word voordat plante voldoende kon herstel. ‘n Verdere moontlikheid is die feit dat slegs een spesie die kamp bewei wat die negatiewe impak van selektiewe weiding versterk. Hierdie probleem is ook sterker aanwesig in gebiede met ‘n lae en wisselvallige reënvalpatroon waar dit vir bestuurders moeilik is om diere op ‘n gereelde basis tussen kampe te roteer. Dit is dus duidelik dat bestuurders ‘n meer buigsame roteringstelsel in plek moet stel en dat hulle die toestand van die grasveld moet ondersoek sodat diere slegs na ‘n nuwe kamp geskuif word indien dit voldoende herstel het van die vorige weidingsperiode. Uit ons ondersoek het dit geblyk dat herbivoorafsluitings uiters nuttig is om die gevolge wat weiding vir die gehalte en samestelling van plante kan inhou te ondersoek. Daar is ook bevind dat beleidsformuleringe, gebaseer op wetenskaplike resultate, as ‘n beter opsie beskou kan word vir hierdie weidingsgebiede.

Sleutelwoorde: fekale profiele, ru-proteïene, fosforiese, weiding, drakrag, plantgehalte, planthoeveelhede, bestuurstipes, habitatsoorte

Contents

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

List of Tables

List of Figures

Acknowledgements

Special thanks go to my supervisors Prof. D.M. Ward and Dr W.S. Watts for all their input and encouragement in my project. I am thankful to NRF, Andrew Mellon Foundation and Ernst and Ethel Eriksen Trust for their financial support for the study. My appreciations to all that contributed in some way for the accomplishment of this study.

I am grateful to Errol and Barbara Tegg; and Charles and Denise Hall for their hospitality, transport during my field visits in Pniel their assistance in many other ways proved invaluable. Appreciations to Elsie Blom who assisted me with fieldwork in scorching sun of Kimberley and many members of the Pniel community who helped in various ways towards my project. I am indebted to the staff of Pniel Estates for help received from them. I am also thankful to students that were involved in Pniel Project especially to Mari-Louise Britz, Georgina Gantana and Tineke Swanepoel, née Kraaij. Special appreciations go to Mari-Louise Britz for encouragements and rewarding discussions during my study in the field and in the department. I am indebted to all my colleagues and staff in the department of Conservation Ecology. Thanks to Monean Heynes and Heidi Thüneman for their administrative and technical support. Special thanks for the translation of an abstract into Afrikaans as required by my institution go to Helena Faasen.

Finally and importantly I would like to thank my favourite aunt, Mrs P.Z. Magojo; my friend, Mrs B.A. Nzoyiya; my neighbour, Ngobe family, my family and all my friends especially from St Pauls Church (Stellenbosch) for their continuing love, encouragement support, and enthusiasm. I could have not done it without them.

Chapter 1

General introduction

In this chapter, the structure of the thesis, general background, problem statement, objectives of this study and the study area are briefly explained. Each chapter of the thesis is written in the format of a manuscript and in accordance of the required format for submission to specific recognized scientific journals. Chapters 2-5 have been submitted and/or have been accepted for publication in journals. Consequently, formats differ among chapters. The name of the journal to which the chapter has been submitted is listed at the beginning of the respective chapters.

The structure of the thesis

Chapter 1 is the current chapter and provides a general introduction to the study. Chapter 2 discusses the effects of grazing, fire, nitrogen and water availability on nutritional quality of grasses in semi-arid savanna, South Africa. This chapter is written in the format of *Rangeland Ecology and Management* and is currently under revision for publication in that journal. Chapter 3 has been submitted for publication in *African Journal of Range and Forage Science*. This chapter describes spatial and temporal variation in plant quantity and quality among management types and habitat types and stocking rates in different management types (commercial, communal and game). Chapter 4 has been submitted for publication in *African Journal of Range and Forage Science* and explores quality and quantity variations inside and outside herbivore exclosure plots among commercial, communal and game management and habitat types in the semi arid savanna. Chapter 5 focuses on using faecal profiling to assess the effects of different management types on diet quality in semi-arid savanna, and has been accepted for the *African Journal of Range and Forage Science* Volume 32: 29-38. Chapter 6 deals with the general conclusions and implications for rangeland policy development.

Background

Many South African farmers are affected by ongoing degradation of natural grazing resources that manifest itself in soil erosion, low land-fertility, poor livestock performance, unproductive areas and bush encroachment (Düvel 1995). It is believed that overstocking, poor management and other anthropogenic impacts are greater on the communal rangelands than on commercial rangelands (Ward et al. 1998). Communal livestock farmers, in particular, are under pressure to overstock in the face of increasing human population pressure and due to reductions in available land area during the apartheid period, resulting in over-utilization of the rangeland. The condition of mammalian herbivores is aggravated in a degraded rangeland because herbivores seldom obtain an optimal diet from a single plant source and must optimize their nutritional and energy requirements by selection of a range of food resources with complementary nutrient concentrations (Robbins 1993). The quantity and quality of plants available to herbivores depend on the balance between the availability of water and soil nutrients (Bell 1982). Unfortunately, little emphasis has been placed thus far on the roles of forage quality and quantity on the sustainability of rangelands in semi-arid savanna, in spite of the fact that large numbers of South Africans depend on rangelands for their livelihoods because some 72% of South Africa is deemed unsuitable for other forms of agriculture.

Problem statement

Arid regions have high spatial and temporal variation in rainfall that causes large fluctuations in plant biomass. Consequently, calculating optimal stocking rates is extremely difficult, a problem, which is compounded when attempts are made to make comparisons among rangelands differing in management type and inherent differences in vegetation, caused by differences in soil type.

Objectives

1. To estimate nutritional value of grass species under various conditions by applying different treatments (water, fire, nitrogen and grazing) in a field experiment.
2. To determine the spatial and temporal variability in the abundance and quality of vegetation over time.
3. To assess veld quality and diet quality of wild game and livestock by faecal profiling
4. To determine variations in forage quality and quantity inside and outside herbivore exclosure plots among management and habitat types in semi-arid savanna
5. To formulate policy based on results obtained from the present study.

Study area

Pniel Estates lies to the northwest of Kimberley in the Northern Cape Province, South Africa (28º 36' S, 24º 32' E). Both soil type and low and erratic rainfall make the Pniel Estates unsuitable for crop cultivation, thereby compelling local people to be livestock, game and cattle ranchers. Therefore, degradation of the rangeland in this area has great potential environmental, social and economic impacts on the Pniel Estates community because it can reduce the carrying capacity of their land. This is an area where an extensive and longer-term project aiming to provide guidelines for the sustainable management of semi-arid savannas is being conducted (http://www.ukzn.ac.za/Biology/PnielProject461.aspx). Pniel Estates covers 25 000 ha and consists of a game ranch, a commercial ranch owned by the Evangelical Lutheran Church and a communal ranch that has domestic livestock (cattle, goats, horses and donkeys). People in the communal portion of Pniel Estates are currently engaged in the process of claiming the land formally from the Evangelical Lutheran Church in terms of the Land Act of 1994, which attempts to rectify the problems of land expropriation caused by the Land Act of 1913. These ranches have different management types in close proximity on the same soil type, making the area appropriate for determination of the impacts of game, communal and commercial ranching in semi-arid savanna. Pniel Estates forms part of the proposed 150 000 ha Kimberley Conservation Triangle, which has much potential as a large conservation area as it has a great diversity of vegetation, game ranches for trophy hunting and ecotourism, Vaalbos National Park, old diamond diggings and interesting history (for e.g. Solomon Tshekiso Plaatjie, the first South African black person to write a novel in English and the first secretary general of the African National Congress grew up on Pniel).

References

Bell RHV 1982. The effects of soil nutrient availability on community structure in African ecosystems. In: Huntley BJ and Walker BH (eds) Ecology of tropical savannas. Springer Verlag, New York. pp 193-216.

Düvel GH 1995. Resistance against stock reduction: A cognitive field analysis. South African Journal of Ecology 24: 45-60.

Robbins CT 1993. Wildlife Feeding and Nutrition. Academic Press, London.

Ward D, Ngairorue BT, Kathena J, Samuels R and Ofran Y 1998. Land degradation is not a necessary outcome of communal pastoralism in arid Namibia. Journal of Arid Environments 40: 357-371.

Chapter 2

The effects of grazing, fire, nitrogen and water availability on nutritional quality of grass in semi-arid savanna, South Africa

Abstract

The impacts of fire and grazing management on grass nutritional quality in semi-arid savannas may depend on inherent variation in rainfall and soil nutrient status. We examined the effects of grazing, fire, nitrogen addition, and watering treatments on the nutritional value of grass in a field experiment in the semi-arid savanna of the Northern Cape, South Africa. Forty-eight plots were used in a completely-crossed randomised block design at 3 sites. Treatments were administered for 2 years and after grass samples of all species in all 48 plots were collected in the end of January (early wet season), March (late wet season) and October (late dry season) during the year of the study. Water addition had no effect on grass quality; biomass, crude protein (CP) yield and phosphorus (P) yield in this semi-arid savanna. Nitrogen addition resulted in increased biomass and gross energy (GE) in the early wet season, as well as elevated levels of CP, GE and CP yield in the late wet season. Grazing alone generally had little effect on grass quality, although grass in grazed plots had higher levels of CP in the late wet season and P in the dry season. Grass biomass was greater in plots protected from grazing. There was more CP and P mass per unit area in fenced plots during the wet seasons. Fire interacted with nitrogen addition and grazing to improve grass quality. Soil nitrogen availability appears to be the most important factor affecting grass-nutrient quality during the wet season in this semi-arid system.

Key Words: Savanna, grass nutritional quality, crude protein, phosphorus, grazing, fire, rainfall

Submitted:

“The effects of grazing, fire, nitrogen and water availability on nutritional quality of grass in semi-arid savanna, South Africa”by Mbatha and Ward, *Rangeland Ecology and Management* and is currently under revision for publication.

Introduction

The nutritional quality of grass in natural grazing land is important for maintaining mammalian herbivores (Wilson 1982, Jones and Wilson 1987), especially free-roaming animals in semi-arid ecosystems. Particularly, because most grazing lands in semi-arid regions have low productivity because of low soil moisture as well as low and erratic rainfall (Smith and Schmutz 1975, Medina 1987, Walker and Knoop 1987). This may result in seasonal shortage and low nutritional value of available grass that can constrain animal production in semi-arid savannas (Bergström and Skarpe 1999, Meissner et al. 1999). Grass chemical composition is used as an index of overall diet quality, although chemical composition of grass varies among species (Norton 1982). Moreover, grass nutritional quality varies with space and time (Norton 1982, Wilson 1982, Jones and Wilson 1987). Generally, if grass or alternative resources are not of sufficient quality to overcome deficiencies in these dietary parameters, wildlife and livestock managers are forced to utilize expensive supplements to minimize nutrient deficiencies and maintain production because low grass quality has a great negative effect on animal performance (Ulyatt 1973, Bransby 1981, Freer 1981).

A number of factors can affect grass quality and, consequently, animal production in semi-arid savannas. Water availability, (Wilson 1982, Milchunas et al. 1995) grazing (McNaughton 1985), fire, (Trollope 1982) and soil quality (Donaldson et al. 1984, Snyman 1998, 2002) have been identified as the major factors affecting nutritional quality of grass in semi-arid savannas.

Rainfall can affect the mineral composition of grass (McDonald et al. 1996). For example, phosphorus appears to be present in higher levels when rainfall is high (Bothma 1989, Scholes and Walker 1993, McDonald et al. 1996). In other studies, wet conditions resulted in low CP concentration and high cell wall content has been observed in grass (Wilson 1982).

Leaf removal by grazing animals has positive direct effects by improving photosynthetic rates, increasing availability of nutrients, reducing water stress for ungrazed plant species, and increasing nitrogen concentration in some plants (Wolfson and Tainton 1999). Negative indirect effects of grazing can occur when animals urinate and defecate on plants, thereby decreasing palatability. In contrast, a positive indirect effect of grazing is the increased accumulation of nitrogen in the soil due to urea from urine and protein from feces (Ross and Tate 1984, Stark et al. 2002). This can result in intensified grazing of particular patches with young, green and more nutritious vegetation, especially in an unburned site. Prolonged grazing of preferred patches in unburned natural grazing lands of savanna has resulted in the disappearance of some grass species over a short period (Andrew 1986).

Fire may eliminate the differences in grass quality between grazed and ungrazed patches by returning the grazed landscape to a more uniform phenological and structural state (Hobbs et al. 1991). Thus, fire may increase the palatability of unpreferred patches, thereby reversing the spatial effects of grazing. There is controversy surrounding the effects of fire on the nutritional quality of grass, although it is usually considered that fire increases grass quality in the short term by removing moribund material but decreases quality if it occurs too frequently because of its negative impact on stored reserves (Trollope 1987, 1999).

Crude protein (CP) content declines with increasing age of forage in plant species (Norton 1982, Meissner et al. 1999). This decline in the level of forage CP levels can pose limitations to forage for mammalian herbivores (Wilson 1982). In all seasons, however, the rate and extent of decline varies with grass species (Norton 1982). High growth potential of grass often results in reduced protein and other nutrient concentrations (Wilson and Minson 1980, Ruess 1987), especially when aboveground biomass is increased and soil nutrient supply is constant. Soil nitrogen availability often limits plant productivity in grasslands (Seastedt et al. 1991) and, consequently, CP content of grass. This problem seems to be particularly acute in semi-arid grasslands where soil nitrogen levels are very low (Wilman 1975). Evidence for this comes from applications of nitrogen fertilizer that normally increase crude protein (CP) concentrations in forage in such ecosystems (Wilman 1975, McDonald et al. 1996, Meissner et al. 1999).

Little is known about the interactions among grazing, fire, soil nitrogen and rainfall and their effects on grass quality in semi-arid savannas in Africa. To date, few studies have simultaneously examined the effects of these factors on grass quality in semi-arid savannas. The objective of this study was to estimate the biomass and nutritional value of grass under different environmental conditions of rainfall, nitrogen addition, fire and different grazing regimes using a completely-crossed experimental design in semi-arid savanna near Kimberley, South Africa. Additionally, we wished to determine which combination of the 4 factors leads to maximal increase in grass quality.

Materials and Methods

Study Area

The study was conducted at three sites on Pniel Estates near Barkly West, 35 km northwest of the city of Kimberley, Northern Cape, South Africa. The three sites are referred to as Driebaken (24°24'16'' E, 28°36'11'' S; 1160 m above sea level), Mannetjies Creche (24°22'45'' E, 28°35' 31'' S; 1150 m above sea level.) and Van der Nest (24°29' E, 28°36'11'' S; 1130 m above sea level). Preliminary study was done and vegetation analyses were used to determine similarity of the study areas. The summer mean annual rainfall (based on 84 annual records, kept since 1884) for Barkly West is 388 mm and is extremely variable (C.V. = 39 %) (Kraaij 2002). The mean temperatures for Kimberley range between 3.2 - 18.2°C in June and 17.9 - 40°C in February with an average of 22 days of frost per year. The soil consists of nutrient-poor Kalahari sand of aeolian and local origin (Bosch 1993), varying from deep red and yellow sand to shallow and stony (Bezuidenhout 1994).

The vegetation type in this semi-arid savanna is known as Kalahari Thornveld (Acocks 1988) or Kimberley Thorn Bushveld (Low and Rebelo 1998). There are scattered trees, mostly *Acacia erioloba*; camelthorn and *A. tortilis;* umbrella thorn. The shrub layer is dominated by *A. mellifera* (blackthorn), *Grewia flava* (velvet raisin) and *Tarchonanthus camphoratus* (wild camphor bush) (Smit 1999). The herbaceous sward mainly consists of tufted perennial grass; the most common species are *Schmidtia pappophoroides* (sand quick grass) and *Eragrostis lehmanniana* (Lehmann’s love grass). The following grass species have a more patchy distribution: *Stipagrostis uniplumis* (silky bushman grass), *Melinis repens* (Natal red top), *Heteropogon contortus* (spear grass), *Aristida diffusa* (iron grass), *A. congesta* (tassel three-awn), *Eragrostis obtusa* (dew grass), *E. superba* (saw-tooth love grass) and *Enneapogon scoparius* (bottlebrush grass) (Russell et al. 1991, van Oudtshoorn 1999). The most common forbs are *Pentzia* and *Asparagus* species.

Field Experiments

The experiment entailed four treatments, each at two levels: (1) maximum-recorded rainfall (800 mm per annum) *vs* natural rainfall; (2) nitrogen addition *vs* no nitrogen addition; (3) burning *vs* no burning; and (4) grazing and/or clipping *vs.* no grazing. A randomized complete-block design with completely-crossed treatment levels was used at each of the three sites, i.e. a design with one replicate per treatment combination at each site (= block) to provide a total of 48 experimental plots (16 plots per site). Plots were 5 m x 5 m in size and spaced within 2 – 10 m of each other. During a preliminary study, optimal plot size of 25 m^2 was determined on the basis of the asymptote of the species-accumulation curve. Experimental plots were placed in areas of similar soil type, vegetation structure, tree and grass cover.

Treatments

Burning

Control plots were protected from burning. Fire-treated plots were burned in October 2000, January 2001, October 2001 and beginning of January 2002. No plots were burned after the end of January 2002 until data collection was completed. Corncobs were soaked in fuel and burned to ignite individual grass tufts to protect control plots from fire. Fuel was not enough for a firebreak.

Grazing and/or Clipping

Plots protected from grazing were fenced off in September 2000 and for the entire study period to exclude livestock and game. Grazed and/or clipped plots were not fenced and were thus exposed to additional grazing by livestock and wild herbivores (such as steenbok, *Raphicerus campestris*; gemsbok, *Oryx gazella*; springbok, *Antidorcas marsupialis* and blue wildebeest, *Connochaetes taurinus*). Grass was clipped monthly between October 2000 and February 2001. Thereafter, grass was clipped in October 2001 and beginning of January 2002. All these clipping treatments were done before grass samples were collected from all 48 experimental plots for the first time in the end of January 2002 for biomass, crude protein (CP), phosphorus (P), gross energy (GE) and dry matter (DM) digestibility analyses.

Nitrogen Addition

Nitrogen fertilizer was spread evenly in plots supplemented with nitrogen during the growing season (January 2001, February 2001, March 2001 January 2002, February 2002 and March 2002). A total of 168 kg N/ha was added in the form of limestone ammonium nitrate (600 kg.LAN/ha) per year. This was regarded as a high rate of nitrogen application in several studies (Le Roux and Mentis 1986, Tilman 1987, Walker and Knoop 1987). The combination of lime and ammonium nitrate was chosen because pure ammonium fertilizer acidifies the soil, resulting in a reduced number of plant species (Goulding et al. 1998). Control plots were protected from nitrogen addition.

Rainfall simulation

Control plots only received natural rain. In addition to natural rain, irrigated plots were supplemented with simulated rain to amount approximately to the 120-year extreme of 800 mm rainfall per annum. Plots supplemented for water addition were irrigated twice a month between October 2000 and April 2001. Then, water supplemented plots were irrigated twice monthly between October 2001 and March 2002. Each irrigation applications added 32 mm over 2 hours per day in addition of natural rainfall. Water was uniformly applied with sprinklers to simulate natural rainfall.

The sequence of treatment applications was as follows: All fire-treated plots were burned. Thereafter, grass in all unfenced plots was cut to ground level. Nitrogen fertilizer was then applied in all nitrogen-treated plots. Lastly, watering was done in all plots supplemented for water addition. The grass samples were collected for biomass and diet quality measurements for the first time from all plots in the end of January 2002. A 1 m x 1 m quadrat was randomly placed twice in each plot and then grass within it was clipped to ground level. Again, grass was clipped at the end of wet season, March 2002 and at the end of dry season in October 2002 for grass biomass, CP, P, GE and dry matter digestibility estimation. Samples included standing dead and live grass. We multiplied the percent concentrations and grass biomass per area and summed the result to calculate the mass of CP and P available per plot.

Laboratory Measurements

Grass samples were collected from each plot and sorted to species. The grass species were air dried in a ventilated room and then transported to the laboratory where they were dried in an oven at 65°C to a constant mass. Different grass species from the same plot were mixed in proportion to their abundance within the plot and milled to pass through a 1 mm mesh screen. Crude protein, GE, P and DM digestibility were assessed. The grass samples were analyzed for CP concentrations using a standard Kjeldahl technique (AOAC 1990). Energy of grass was assessed by standard bomb calorimetry. The DM digestibility of grass species was assessed by the *in vitro* digestible dry matter method of Zacharias (1986) because this technique incorporates concentrations, ratios and structures of forage constituents in an index of potential for breakdown by rumen microbial populations (Milchunas et al. 1995). Phosphorus content was ascertained spectrophotometrically according to the micro technique of the AOAC (1990).

Statistical Analysis

Analysis of variance of data from the diet quality was conducted using a general linear model (GLM) procedure of *Statistica* (v.6, 1984-2004 Statsoft Inc.) for the completely-crossed randomized block design, with site as a blocking factor.

Results

Early growing season

A significant effect ($P = 0.04$) of nitrogen addition was observed on grass biomass (Table 2.1 and 2.2). Similarly, grazing and/or clipping had a significant difference ($P < 0.001$) on grass biomass (Table 2.1 and 2.2).

Also, nitrogen addition had significant effects (P = 0.04) on GE level of grass (nitrogen addition 18.74 MJ/kg ± 0.22; no nitrogen addition 17.95 MJ/kg ± 0.30 (mean ± SE)) (Table 2.1). The interaction of fire and nitrogen had a significant influence (P = 0.01) on grass CP content (Table 2.1 and 2.3, Fig. 2.1). The interaction between fire and grazing and/or clipping on grass DM digestibility was not significant (P = 0.054) significantly Table 2.1 and 2.3, Fig. 2.2). The only factor that had a significant effect (P = 0.02) on P content of grass was fire (fire 1.03% ± 0.08; no fire 0.08% ± 0.05 (mean ± SE)) (Table 2.1).

Grass CP and P yields showed a strong significant and positive correlation on grass biomass (r = 0.8, P = 0.001). Grazing and/or clipping showed a significant effect (P = 0.04) on grass CP yield and (P < 0.001) on grass P yield (Table 2.1 and 2.2).

Table 2.1. Significant results of analysis of variance of the effects of fire, grazing, and nitrogen addition on biomass, crude protein (CP), CP yield, gross energy (GE), dry matter (DM) digestibility phosphorus (P) and P yield of grass.

Season	Dietary parameters	Effect	F	p
Early wet	Biomass (g/m^2)	Nitrogen	6.7228	0.04
	Biomass (g/m^2)	Grazing	36.65	< 0.001
	GE (MJ/kg)	Nitrogen	4.421	0.04
	CP (%)	Fire *Nitrogen	6.8260	0.01
	DM digestibility (%)	Fire *grazing	4.008	0.054
	P (%)	Fire	5.5808	0.02
	CP yield (kg/m^2)	Grazing	9.79	0.04
	P yield (kg/m^2)	Grazing	18.18	< 0.001
Late wet	CP (%)	Nitrogen	34.712	< 0.001
	GE (MJ/kg)	Nitrogen	5.80	0.02
	CP (%)	Grazing	4.991	0.03
	P (%)	Grazing	39.833	< 0.001
	CP (%)	Fire*grazing	9.937	0.003
	CP yield (kg/m^2)	Fire*Grazing	5.15	0.03
	P (%)	Fire*Nitrogen	5.739	0.02
	Biomass (g/m^2)	Grazing	36.04	< 0.001
	CP yield (kg/m^2)	Grazing	21.26	< 0.001
	P yield (kg/m^2)	Grazing	15.62	< 0.001
	CP yield (kg/m^2)	Nitrogen	15.05	< 0.001
Late dry	P (%)	Grazing	40.60	< 0.001
	DM digestibility (%)	Fire	11.164	0.002

Late growing season

Addition of nitrogen had a highly significant difference (P < 0.01) on grass CP content (nitrogen addition 7.06% ± 0.31; no nitrogen addition 4.92% ± 0.28 (mean ± SE)) (Table 2.1). Also, nitrogen addition showed a significant positive effect (P = 0.02) on GE level of grass (nitrogen addition 17.17 MJ/kg ± 0.09; no nitrogen addition 16.89 MJ/kg ± 0.09 (mean ± SE)) (Table 2.1). A significant difference (P = 0.03) of grazing and/or clipping was observed on grass CP content (grazing and/or clipping 6.39% ± 0.06; no grazing and/or clipping 5.58% ± 0.05 (mean ± SE)); (Table 2.1 and 2.2). Similarly, a significant difference (P < 0.001) of grazing on grass P concentration was noticed (grazing 0.76% ± 0.04; no grazing 0.68% ± 0.04 (mean ± SE)) (Table 2.1). The interaction between grazing and/or clipping and fire showed a significant influence on grass CP content (P = 0.003; Fig. 2.3) and CP yield (P= 0.03, Fig. 2.4) and (Table 2.1 and 2.3). Fire and nitrogen interacted and resulted in a significant effect (P = 0.02) on grass P content (Table 2.1and 2.3, Fig. 2.5). Grazing and/or clipping showed a significant difference on grass biomass (P < 0.001), CP yield (P < 0.001) and P yield (P < 0.001); (Table 2.1 and 2.2). Similarly, a significant effect (P < 0.001) of nitrogen addition was observed on grass CP yield (Table 2.1 and 2.2).

Table 2.2: Mean ± SE of grass biomass, CP yield and P yield in the early wet, late wet and late dry seasons. Bold = significant values.

Season	Treatment	Biomass (g $^{m-2}$)	CP yield (g $^{m-2}$)	P yield (g $^{m-2}$)
Early wet	Natural rain	69.72 ± 5.91	0.65 ± 0.10	0.006 ± 0.001
	Added water	78.44 ± 5.92	0.76 ± 0.10	0.008 ± 0.001
	No N_2 addition	**58.59 ± 7.44**	0.65 ± 0.11	0.07 ± 0.001
	N_2 addition	**99.57 ± 7.44**	0.76 ± 0.11	0.008 ± 0.001
	No burning	74.65 ± 7.52	0.70 ± 0.11	0.006 ± 0.001
	Burning	73.52 ± 7.52	0.71 ± 0.11	0.008 ± 0.001
	No grazing	**99.41 ± 7.19**	**1.00 ± 0.10**	**0.01 ± 0.001**
	Grazing	**48.75 ± 2.40**	**0.42 ± 0.10**	**0.00 ± 0.001**
Late wet	Natural rain	73.73 ± 6.37	0.45 ± 0.04	0.0005 ± 6^{-5}
	Added water	83.25 ± 6.37	0.46 ± 0.04	0.0006 ± 6^{-5}
	No N_2 addition	75.79 ± 6.37	**0.35 ± 0.04**	0.0005 ± 6^{-5}
	N_2 addition	81.18 ± 6.37	**0.56 ± 0.04**	0.0006 ± 6^{-5}
	No burning	77.18 ± 6.37	0.42 ± 0.04	0.0005 ± 6^{-5}
	Burning	79.79 ± 6.37	0.49 ± 0.04	0.0006 ± 6^{-5}
	Grazing	**105.55 ± 6.37**	**0.58 ± 0.04**	**0.0007 ± 6^{-5}**
	No grazing	**51.43 ± 6.37**	**0.332 ± 0.04**	**0.0004 ± 6^{-5}**
Late dry	Natural rain	36.10 ± 2.98	0.51± 0.11	0.0001 ± 1^{-5}
	Added water	37.91 ± 2.98	0.65 ± 0.11	0.00012 ± 1^{-5}
	No N_2 addition	34.71 ± 2.98	**0.37 ± 0.11**	0.00011 ± 1^{-5}
	N_2 addition	39.30 ± 2.98	**0.79 ± 0.11**	0.00012 ± 1^{-5}
	No burning	38.11 ± 2.98	0.50 ± 0.11	0.00012 ± 1^{-5}
	Burning	35.90 ± 2.98	0.67 ± 0.11	0.00011 ± 1^{-5}
	Grazing	**47.34 ± 2.98**	0.72 ± 0.11	0.00011 ± 1^{-5}
	No grazing	**26.67 ± 2.98**	0.50 ± 0.11	0.00011 ± 1^{-5}

End of dry season

Burning had positive and significant effects (P = 0.002) on grass DM digestibility (fire 31.82% ± 2.15; 22.7% ± 1.81(mean ± SE)) (Table 2.1). Grazing had a significant effect (P < 0.001) on P level of grass (grazing and/or clipping 0.45% ± 0.03; no grazing and/or clipping 0.24% ± 0.01 (mean ± SE)) (Table 2.1). In this season, all other factors showed a non-significant effect on grass CP, GE, biomass, CP yield and P yield. For all seasons, a non-significant effect (P > 0.05) of rain on all dietary parameters was observed.

Table 2.3. Mean ± SE of significant interaction effects on grass CP, P, DM digestibility and CP yield during the study period.

Season	Treatment 1	Treatment 2	Dietary parameter	Mean ± SE
Early wet season	Fire	Nitrogen	CP (%)	
	0	0		7.99 ± 1.21
	0	1		10.61 ± 1.21
	1	0		10.51 ± 1.21
	1	1		7.54 ± 1.21
	Fire	Grazing	DM digestibility (%)	
	0	0		24.73 ± 3.40
	0	1		31.60 ± 3.40
	1	0		31.22 ± 3.40
	1	1		24.46 ± 3.40
Late wet season	Fire	Grazing	CP yield (kg/m^2)	
	0	0		481.70 ± 54.13
	0	1		354.99 ± 54.13
	1	0		682.11 ± 54.13
	1	1		309.58 ± 54.13
	Fire	Grazing	CP (%)	
	0	0		4.73 ± 0.38
	0	1		6.69 ± 0.38
	1	0		6.43 ± 0.38
	1	1		6.109 ± 0.38
	Fire	Nitrogen	P (%)	
	0	0		0.0065 ± 0.0005
	0	1		0.0075 ± 0.0005
	1	0		0.0081 ± 0.0005
	1	1		0.0066 ± 0.0005

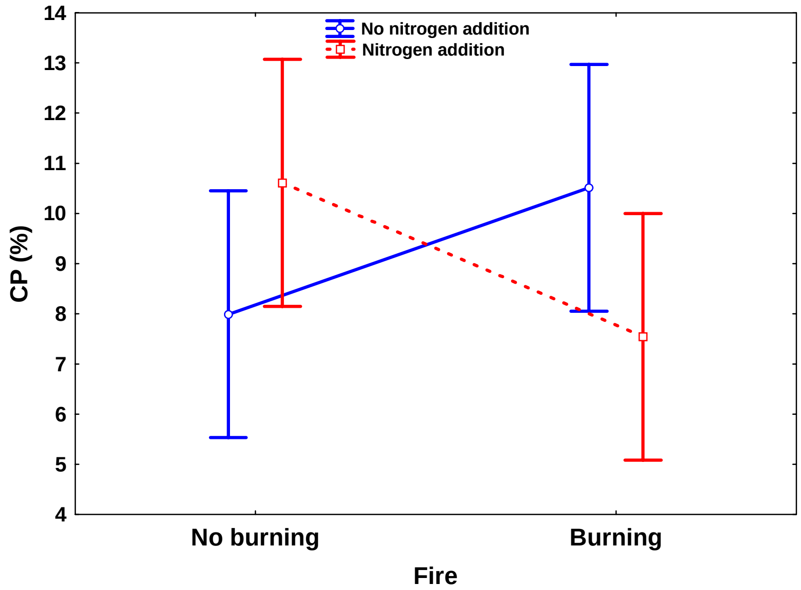

Fig. 2.1. Interaction effect of nitrogen and fire on grass CP level in the early wet season. Vertical bars denote 95% confidence intervals. Squares and dashed lines = nitrogen addition and circles and solid lines = no nitrogen addition.

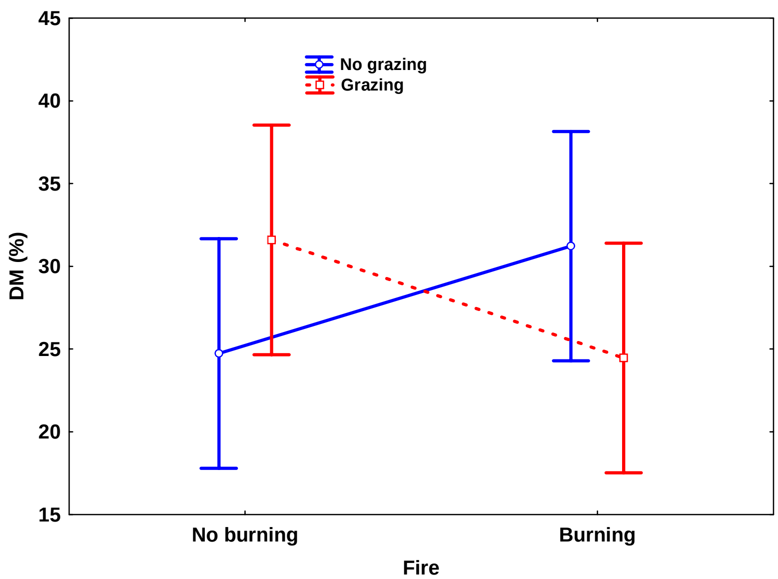

Fig. 2.2. Interaction effect of nitrogen and fire on grass DM digestibility level in the early wet season. Vertical bars denote 95% confidence intervals. Squares and dashed lines = nitrogen addition and circles and solid lines = no nitrogen addition.

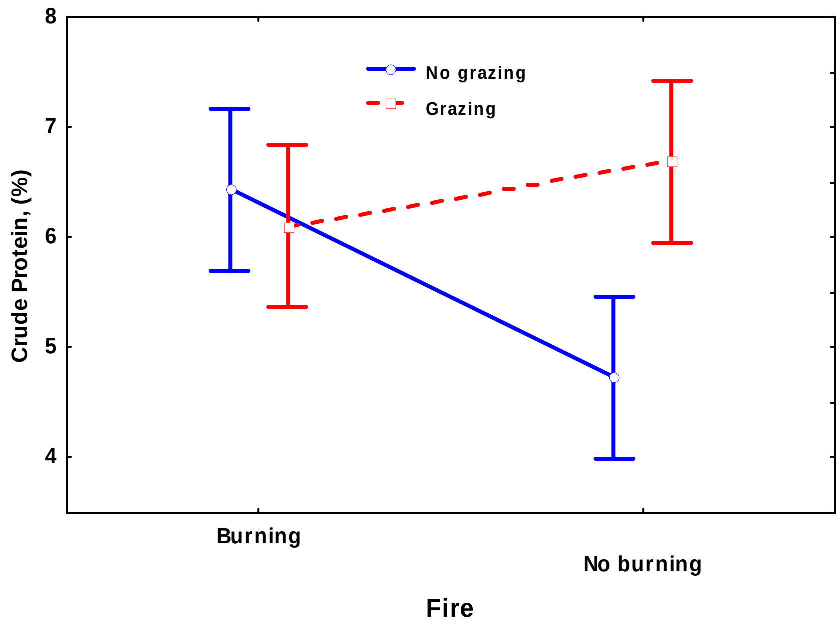

Fig. 2.3. Interaction between grazing and fire on grass CP level in the late wet season. Vertical bars denote 95% confidence intervals. Squares and dashed lines = grazing and circles and solid lines = no grazing.

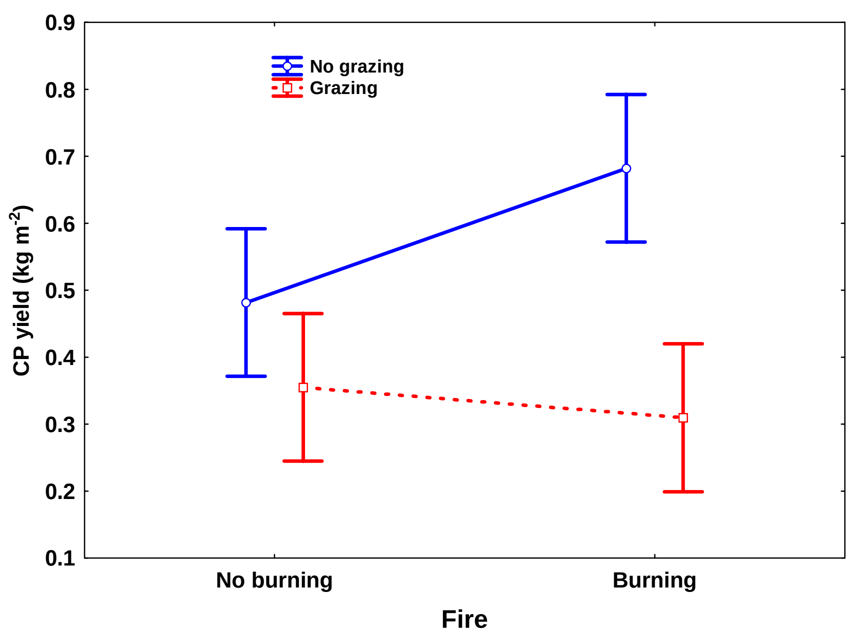

Fig. 2.4. Interaction between grazing and fire on grass CP yield in the late wet season. Vertical bars denote 95% confidence intervals. Circles and solid lines = no grazing and squares and dashed lines = grazing.

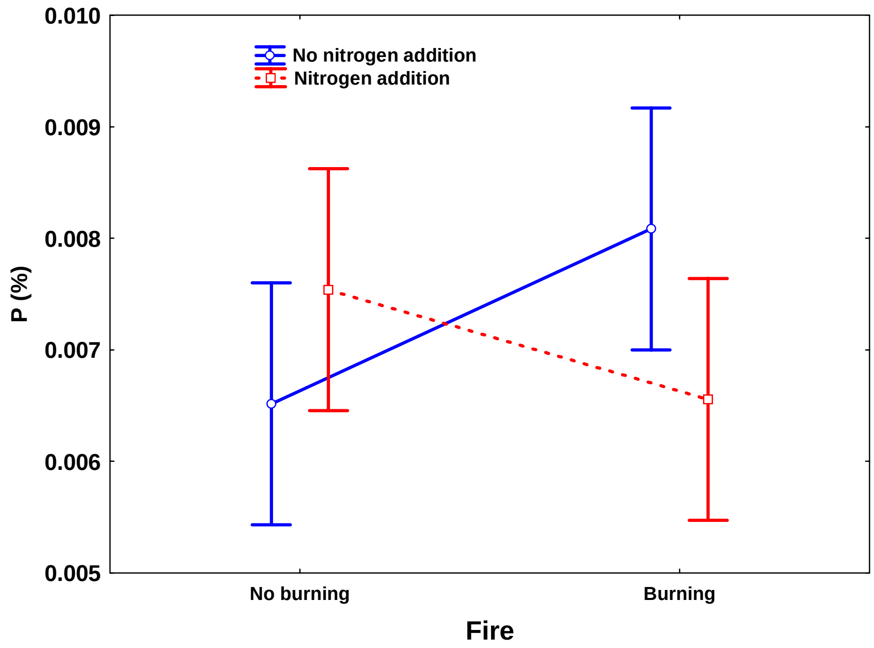

Fig. 2.5. Nitrogen and fire on grass P concentration in the late wet season. Vertical bars denote 95% confidence intervals. Squares and dashed lines = no burning and circles and solid lines = burning.

Discussion

The effects of grazing and/or clipping

The fenced plots had more grass biomass than unfenced plots, especially in the wet seasons. This is attributed to grazing when grass is young and palatable because it directly reduced available grass biomass. Similarly, grazing had a negative influence on grass CP and P yield when grass was young and green during the wet seasons. Current grazing and grazing of previous years decreased grass biomass and CP yield as also observed by (Hobbs et al. 1991). Similarly, Turner et al. (1993) in prairie grassland found that CP and P yield was greater in fenced plots than in unfenced plots where grazing was excluded for 10 years before the experiment was conducted. However, similar to our results, Milchunas et al. (1995) in semi-arid grassland, Ritchie et al. (1998) in oak savanna and Willms et al. (2002) in mixed prairie observed that nitrogen yields were greater in ungrazed plots compared to grazed plots. The results of Milchunas et al. (1995) were mostly attributed to changes in species composition and differences in soil nitrogen dynamics during a long term (approximately 50 years) of light grazing, heavy grazing and no grazing treatments. In our study, the improved CP and P mass in ungrazed plots may be mainly due to a positive correlation between leaf biomass and protein and mineral composition (see also Norton 1982). This may be true for grass when leaves are young and green with high nutrient levels (Downing 1979, Gillon 1983, Holland and Detling 1990), as was also observed in our study. However, when grass was moribund, there may be a negative correlation between leaf percentage of grass and nutritive values. In the present study, grass quality (CP, P, GE and DM digestibility) was greatest when young and green grass had high biomass. This trend changed in the dry season when grass was moribund; biomass was determined to be low (Table 2.2) and grass quality decreased.

Grazing mammalian herbivores remove plant biomass periodically during the wet season (Knapp and Seastedt 1986, Ruess 1987) and dry season. Thus, the quality of plant litter returned to soil is improved by grazing mammalian herbivores due to deposition of nitrogen-rich urine and feces (Ross and Tate 1984, Day and Detling 1990, Pastor and Naiman 1992, Russelle 1992, Augustine and McNaughton 1998, Stark et al. 2002). Eventually, nutrient uptake by plants from the soil is increased (Ruess 1984) and shoot nitrogen content in many types of grassland is improved (Holland and Detling 1990, Turner et al. 1993, Milchunas et al. 1995, Knapp et al. 1999). Therefore, a significant positive effect of grazing in the late wet season on grass CP levels may result from consistent grazing that reduces aboveground biomass. Crude protein concentration gradually declined as the season progressed from the wet season to the dry season, indicating that during the vegetative stage of grass, protein levels are high and later decline as plants approach maturity, eventually posing a limitation to forage quality for grazing animals (Norton 1982). Also, the improvement of CP levels in clipped and/or grazed than unclipped plots during the late wet season can be attributed to morphological changes resulting from canopy closure in unclipped and/or ungrazed plants (Knapp and Seastedt 1986, McNaughton 1992). This elevation in grass CP content could also support increased photosynthetic rates, which is a compensatory response in grass (Caldwell et al. 1981, Detling and Painter 1983, Wallace et al. 1984, Senock et al. 1991). Post-grazing augmentation of photosynthesis is due to increased light availability for all species in grazed patches and greater tissue nitrogen level in the leaves as nitrogen is reallocated from roots (Knapp et al. 1999) (although nitrogen reallocation was not measured in this study). During the dry season, grazing did not result in enhanced CP levels.

In immature stages, grass stems are more digestible than the leaves, but with advancing maturity, the digestibility of the leaf fraction declines very slowly while that of the stem declines rapidly (Wilson 1982, McDonald et al. 1996). As the grass matures, the stem comprises an increasing proportion of total herbage and hence has a much greater influence on the digestibility of the whole plant than do the leaves (Norton 1982). We observed that in the early wet season fire and grazing interaction improved *in vitro* digestibility, which resulted in enhanced GE level of grass. This enhanced grass DM digestibility was observed during the wet seasons while the grass was young, growing and had less fiber after fire and grazing treatments. Thus, the interaction of fire and grazing improved grass DM digestibility and GE because both fire and grazing reduce grass biomass.

Clipped and/or grazed plots showed a positive increased phosphorus (P) level of grass in the late wet and dry seasons, although P concentrations decreased gradually from wet season to dry season. These results indicate that grazing continuously reduced the aboveground biomass, resulting in less aboveground biomass of grass to share the available P content, thereby resulting in enhanced grass P level in the clipped and/or grazed plots. Thus, grazing and/or clipping does not have a strong effect on grass P concentration because it did not improve P levels in the wet season. However, in the late dry season, P levels in grazed plots increased at a time when grass P levels were generally very low (mainly due to the age of the plants). This positive effect of grazing in the late growing season may enhance palatability of dry grass because P content improves palatability (Downing 1979).

The effects of fire

Our results are not consistent with observations by Mitchell et al. (1994) in that the interaction effect of nitrogen addition and fire improved grass CP content in the early wet season. Fire removed the dead old grass, resulting in young growth of grass tissue. Moreover, nitrogen addition to the soil enhanced grass CP level of sprouting, young and green grass that grew after burning and whose photosynthetic rate is high. According to Allen et al. (1976), Christensen (1977), Tainton et al. (1977), Gillon (1983), Griffin and Friedel (1984), McNaughton (1985) and Frost and Robertson (1987) the interaction of fire and nitrogen addition resulted in young grass leaves richer in CP content than grass in unburned plots with no nitrogen addition whose CP levels steadily declined while their digestible material increased. Contrastingly, in our study the interaction of fire and nitrogen resulted in low CP levels. Also, burning failed to increase grass CP in our study which accords with Allen (1976) due to enhanced losses of nitrogen from fire (Hayes and Seastedt 1989).

Dry matter digestibility and CP concentrations tend to be higher in young and green grass tissues than in older and mature plant tissues (Norton 1982). Crude protein concentrations were improved by the interaction of fire and grazing in the late wet season. This positive effect of fire and grazing interaction is not surprising as both factors induce new growth by removing plant biomass, albeit at different plant stages (Gillon 1983, Johnson and Matchett 2001). Fire and grazing counteracted, thus the interaction of both did not improve the P levels of grass in the late wet season.

The significant increase in grass P levels after fire in the early wet season is similar to the findings of Noller et al. (1985). This may be due to the high concentration of minerals in ash mobilized in rainwater at the beginning of the wet season when rainfall is high (Holt and Coventry 1990, McDonald et al. 1996). However, there is controversy about the effect of ash improving grassland nutrients; few studies have been conducted to clarify this process. According to Raison (1979), the quantity of nutrients released by burning savanna grasslands is a smaller portion than that released by burning forests. Moreover, ash resulting from burnt grassland may be insufficient to cover the soil (Jordan 1965). In our study, the ash and, perhaps, rain may have enhanced the P concentrations because the natural mean rainfall of 2001/2002 was 29% more than the annual mean rainfall. Thus, P in the atmosphere, in the form of ash residues, may have been deposited back in the soil by heavy natural rain thereby raising soil nutrients. However, there were no significant effects of rain or interactions between rain and other factors on all nutrient parameters measured in the present study. Also, after burning, the sprouting young grass leaves are richer in P than the older leaves in unburned plots, whose P levels steadily decrease with age (Christensen 1977, Gillon 1983). A non-significant effect of fire on the nutrition of grass late in the wet season corresponds with the results reported by Christensen (1977), Noller et al. (1985) and Van de Vijver et al. (1999).

In the late dry season, fire had a positive effect on DM digestibility because grass in burned plots was younger than in unburned plots. Consequently, grass in plots treated with and without fire is of different biological age (Gillon 1983). Therefore, in burned plots, leaves are younger, with low cell wall constituents (such as cellulose and lignin) and, consequently, have enhanced grass DM digestibility even in the dry season (McDonald et al. 1996). Moreover, burning can prolong the green-growth periods and expose new growth to herbivores by removing the old growth (Vallentine 2001). Thus, mammalian herbivores can digest grass from burnt plots better than grass in unburned plots, even in the dry season when most of the nutrients are low.

The effects of nitrogen supplementation

Grass responded to nitrogen supplementation through growth resulting in increased grass biomass as also observed by Jones and Wilson (1987). Fertilizer application may also improve the efficiency of grassland production (Ruess 1987) by positively affecting the nutrient quality of grass (Hamilton et al. 1998, Wolfson and Tainton 1999, McDonald et al. 1996). In the late wet season, nitrogen addition had a positive influence on CP content and CP yield of grass, consistent with the results of Grünow et al. (1970), Allen et al. (1976), Jones and Wilson (1987), Mitchell et al. (1994) and Cohen et al. (2004). According to Seastedt et al. (1991) and Blair (1999) nitrogen availability limits plant productivity in grasslands. Plots with nitrogen addition had increased plant productivity. Thus, this may indicate that nitrogen may limit growth of grass in this semi-arid savanna.

The interaction of nitrogen addition and fire did not improve CP content in the early wet season and P levels in the late wet season while grass was young and green. This may be due to the time when fire and nitrogen were applied. All positive effects of nitrogen addition were observed during the wet seasons when grass was young and green. When grass leaves were mature and/or not green, rate of photosynthesis was reduced and nutrient extraction from the soil was low or zero. Consequently, nitrogen application did not improve grass-nutrient quality in the dry season. This may also be explained by that soil mineralization rates are high when dry savanna soil is first moistened, but drop to low levels if soil remains moist (McNaughton 1985). Thus, low levels of nutrients are observed in the dry season. Furthermore, leaf senescence is often associated with nitrogen deficiency as a result of remobilization of nitrogen (Wolfson and Tainton 1999).

Nitrogen supplementation does not directly improve digestibility other than through its influence on growth rate and the stage of maturity of the plants (Raymond 1969). Thus, application of fertilizer improves forage quality by stimulating the growth of young digestible leaf and stem (Norton 1982). This low fiber content increased the levels of grass GE because grass is affected by the amount of dietary fiber it contains (McDonald et al 1996). Thus, the observed enhancement of grass GE by nitrogen addition in the early and late wet seasons may be indirectly attributed to the high DM digestibility of the young age of these grass parts.

The effects of rain

The quantity and quality of plants available to herbivores depend on the balance between the availability of water and soil nutrients (Le Houérou et al. 1988). Grass growth is rapid during the wet season (McDonald et al. 1996), resulting in high plant biomass (Wilson 1982, Le Houérou 1984, Ruess 1987, Varnamkhasti et al. 1995). Water alone is usually more important for plant biomass or growth than soil nutrients because there is usually leaching of nutrients after high rainfall and, consequently, reduced forage quality (Ruess 1987). In the present study, plots with simulated rainfall surprisingly did not have higher grass biomass and quality than plots receiving natural rain only. Nutrient limitation of the sandy soil type of the study area may have contributed to non-improvement of grass quality and quantity in plots with increased rainfall. Another possible explanation is that grass biomass and quality are non-linearly related to rainfall in above-average rainfall years (as was the case in this study), although this seems unlikely. Further studies are required to tease out the effects of rainfall and other factors in semi-arid African savannas. .

Species composition effects

Analysis of grass quality was done at the plot level by using a mixture of grass from each plot in proportion to their relative abundances. Because this was a relatively short-term study, there was insufficient time for grass species composition to change in response to the treatments (Ward, unpublished data). Consequently, we believe that it is unlikely that we have confounded differences in quality among species in particular plots with differences in quality due to our treatments. Clearly, it would have been optimal to compare each grass species across each treatment combination, but such grass species x treatment combinations did not exist for all combinations or plots due to our randomization procedure for treatments at the beginning of the study. We believe that possible confounding effects of grass species composition differences among plots were minimized because most plots contained 2 species (*Eragrostis lehmanniana* and *Schmidtia pappophoroides*).

Conclusions

Surprisingly, water addition had no effect on grass-nutritional value and aboveground biomass. There was more grass biomass and CP and P mass per area in ungrazed plots during the wet seasons. Nitrogen addition was important, but only during the wet seasons, probably because of uptake limitation in the dry season. Nitrogen addition is seldom done in South Africa, but may be profitable, especially on smaller ranches. In this semi-arid system, fire interacted with nitrogen and grazing to improve grass quality. Grazing alone had little effect on grass quality, although in the late wet season, CP and P levels were high on grazed plots. Both fire and grazing remove grass, albeit at different grass ages, resulting in improved nutrition of grass due to the increase of young, actively-growing grass in the sward that is unobstructed by standing dead grass tissue. The results of this short-term study showed that fire had more positive effects on grass quality than did grazing.

Literature Cited

Acocks, J.P.H. 1988. Veld types of South Africa. Botanical Research Institute, Department of Agriculture and Water Supply, Pretoria.

Allen, L.J., L.H. Harbes, R.R. Schalles, C.E. Owensby, and E.F. Smith. 1976. Range burning and fertilizing in relation to nutritive value of bluestem grass. J. Range Manage. 29:306-308.

Andrew, M.H. 1986. Use of fire for spelling monsoon tallgrasss pasture grazed by cattle. Trop. Grassl. 20:66-77.

AOAC, 1990. Official Methods of Analysis, 15th ed. Association of Official Analytical Chemists. Arlington, USA.

Augustine, D.J. and S.J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. J. Wildl. Manage. 62:1165–1183.

Bergström, R. and C. Skarpe. 1999. The abundance of large wild herbivores in semi-arid savanna in relation to seasons, pans and livestock. Afr. J. Ecol. 37:12-26.

Bezuidenhout, H. 1994. An ecological study of the major vegetation communities of the Vaalbos National Park, Northern Cape. 1. The Than-Droogeveld section. Koedoe 37:19-42.

Blair, J.M. 1999. Fire, N availability, and plant response in grasslands: A test of the transient maxima hypothesis. Ecology 78:2359-2368.

Bosch, P.J.A. 1993. Geological survey: The geology of the Kimberley area. Explanation of sheet 2824. Scale 1:250 000*.* Department of Mineral and Energy Affairs, Republic of South Africa. Government Printer, Pretoria.

Bothma, J. du P. 1989. Mineral deficiencies. p. 561-567. *In*: Bothma, J. du P. (Ed) Game Ranch Management. Van Schaik, Pretoria.

Bransby, D.I. 1981. The value of veld and pasture as animal feed. p. 173-214. *In*: N.M. Tainton, (ed.), Veld and pasture management in South Africa. Shuter and Shooter, Pietemaritzburg.

Caldwell, M.M., J.H. Richards, D.A. Johnson, R.S. Nowak, and R.S. Dzurec. 1981. Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. Oecologia 50:14-24.

Christensen, N.L. 1977. Fire and soil-plant nutrient relations in a pine-wiregrass savanna on the coastal plain of North Carolina. Oecologia 31:27-44.

Cohen, R.D.H., S.B.M. Wright, L.R. Thomas, W.P. McCaughey, and M.D. Howard. 2004. Current and residual effects of nitrogen fertilizer applied to grass pasture on production of beef cattle in central Saskatchewan. Can. J. Anim. Sci. 84:91-104.

Day, T.A. and J.K. Detling. 1990. Grassland patch dynamics and herbivore grazing preference following urine deposition. Ecology 71:180-188.

Detling, J.K. and E.L. Painter. 1983. Defoliation responses of western wheatgrass populations with diverse histories of prairie dog grazing. Oecologia 57:65-71.

Donaldson, C.H., G. Rootman, and D. Grossman. 1984. Long term nitrogen and phosphorus application on veld. J. Grassl. Soc. Sth. Afr. 1:27-32.

Downing, B.H. 1979. Grass protein content and soils as factors affecting area-selective grazing by wild herbivores in the Umfolozi Game Reserve, Zululand. Proc. Grassl. Soc. Sth Afr. 14:85-88.

Freer, M. 1981. The control of food intake by grazing animals. p. 105-124. *In*: R.H.W. Morely (ed.), Grazing animals Elsevier, Oxford.

Frost, P.G.H. and F. Robertson. 1987. The ecological effects of fire in savannas. p. 93-140. *In*: B.H Walker (ed.), Determinants of tropical savannas. IRL Press Limited, UK.

Gillon, D. 1983. The fire problem in tropical savannas. p. 617-641. *In*: F. Bouliere. (ed.) Ecosystems of the World Vol 13: Tropical savannas. Elserview Science, Amsterdam.

Goulding, K.W.T., N.J. Bailey, N.J. Bradbury, P. Hargeaves, M. Howe, D.V. Murphy, P.R. Poulton, and T.W. Willison. 1998. Nitrogen deposition and its contribution to nitrogen cycling and associated soil processes. New Phytol. 139:49-58.

Griffin, G.F. and M.H. Friedel. 1984. Effects of fire on central Australian rangelands. I. Fire and fuel characteristics and changes in herbage and nutrients. Aust. J. Ecol. 9:381-393.

Grünow, O.J., A.J. Pienaar and C. Breytenbach. 1970. Long term nitrogen application to veld in South Africa. Proc. Grassl. Soc. Sth. Afr. 5:75-90.

Hamilton III, E.W., M.S. Giovannini, S.A. Moses, J.S. Coleman, and S.J. McNaughton. 1998. Biomass and mineral element responses of a Serengeti short-grass species to nitrogen supply and defoliation: compensation requires a critical (N). Oecologia 116**:**407–418.

Hobbs, N.T., D.S. Schimel, C.E. Owensby, and D.S. Ojima. 1991. Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. Ecology 72:1374-1382.

Holland, E.A. and J.K. Detling. 1990. Plant response to herbivory and belowground nitrogen cycling. Ecology 71:1040-1049.

Holt, J.A. and R.J. Coventry. 1990. Nutrient cycling in Australian savannas. J. Biogeogr. 17:427-432.

Johnson, L.C. and J.R. Matchett. 2001. Fire and grazing regulate belowground processes in tallgrass prairie. Ecology 82:3377-3389.

Jones, D.H. and A.D. Wilson. 1987. Nutritive quality of forage. p. 65-89. *In*: J.B. Hacker and J.H. Ternouth (eds), The nutrition of herbivores. Academic Press, Sydney.

Jordan, C.F. 1965. Fire influences in old fields of New Jersey Piedmont. N. J. Acad. Sci. Bull. 10:7-12.

Knapp, A.K. and T.R Seastedt. 1986. Detritus accumulation limits productivity of a tallgrass prairie. Bioscience 36:662-668.

Knapp, A.K., J.M. Blair, J.M. Briggs, S.L. Collins, D.C. Hartnett, L.C. Johnson, and E.G. Towne. 1999. Keystone role of bison in North American tallgrass prairie. Bioscience 49:39-5.

Kraaij, T. 2002. Effects of rain, nitrogen, fire and grazing on bush encroachment in semi-arid savanna, South Africa. M.Sc. Thesis. University of Stellenbosch, South Africa.

Le Houérou, H.N. 1984. Rain use efficiency: a unifying concept in arid-land ecology. J. Arid Environ. 7:213-247.

Le Houérou, H.N., R.L. Bingham, and W. Skerbek. 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. J. Arid Environ. 15:1-18.

Le Roux, N.P. and M.T. Mentis. 1986. Veld compositional response to fertilization in the tall grassveld of Natal. S. Afr. J. Plant Soil 3:1-10.

Low, A.B. and A.T.G. Rebelo. 1998. Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria.

McDonald, P., R.A. Edwards, J.F.D. Greenhalgh, and C.A. Morgan. 1996. Animal nutrition, 5th ed. Longman, U.K.

McNaughton, S.J. 1985. Ecology of grazing ecosystems: the Serengeti. Ecol. Monogr. 55:259-294.

McNaughton, S.J. 1992. Laboratory simulated grazing: interactive effects of defoliation and canopy closure on Serengeti grasses. Ecology 73:170-182.

Medina, E. 1987. Requirements, conservation and cycles of nutrients in the herbaceous layer. p. 39-65. *In*: B.H. Walker (ed.), Determinants of Tropical Savannas. IRL Press Limited, UK.

Meissner, H.H., P.J.K. Zacharias, and P.J. O'Reagain. 1999. Forage quality (Feed value). p. 139-168. *In:* N.M. Tainton (ed.), Veld management in South Africa. University of Natal Press, Pietermaritzburg.

Milchunas, D.G., A.S. Varnamkhasti, W.K. Lauenroth, and H. Goetz. 1995. Forage quality in relation to long-term grazing history, current-year defoliation, and water resource. Oecologia 101:366-374.

Mitchell, R.B., R.A. Master, S.S. Waller, K.J. Moore, and L.E. Moser. 1994. Big bluestem production and forage quality responses to burning date and fertilizer in tallgrass prairies. J. Prod. Agric. 73:355-359.

Noller, B.N., N.A. Currey, P.J. Cusbert, M. Tuor, P. Bradley, and A. Harrison. 1985. Temporal variability in atmospheric nutrient flux to the Magel and Nourlangie Creek system, Northern Territory. Proc. Ecol. Soc. Aust. 13:21-31.

Norton, B.W. 1982. Differences between species in forage quality. p. 89-109. *In*: J.B. Hacker (ed.), Nutritional limits to animal production from pastures. Commonwealth Agriculture Bureaux: Farnham Royal, UK.

Pastor, J. and R.J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. Am. Nat. 139:690-705.

Raison, R.J. 1979. Modification of the soil environment by vegetation fires with particular reference to nitrogen transformations: a review. Plant Soil 51:73-108.

Raymond, W.F. 1969. The nutritive value of forage crops. Adv. Agron. 21:1-108.

Ritchie, M.E., D. Tilman and J.M.H. Knops. 1998. Herbivory effects on plants and nitrogen dynamics in oak savanna. Ecology 79:165-177.

Ross, D.J. and K.R. Tate. 1984. Microbial biomass in soil: effects of some experimental variables on biochemical estimations. Soil Biol. Biochem. 16:161-167.

Ruess, R.W. 1984. Nutrient movement and grazing experimental effects on clipping and nitrogen source on nutrient uptake in *Kyllinga nervosa*. Oikos 43:183-188.

Ruess, R.W. 1987. The role of large herbivores in nutrient cycling of tropical savannas. p. 67-91. *In*: B.H. Walker (ed.), Determinants of tropical savannas. IRL Press Limited, UK.

Russell, G.E., L.Watson, M. Koekemoer, L. Smook, N.P. Barker, H.M. Anderson and M.J. Dallwitz. 1991. Grasses of southern Africa. Botanical Research Institute, South Africa.

Russelle, M.P. 1992. Nitrogen cycling in pasture and range. J. Prod. Agric. 5:13-23.

Scholes, R.J. and B.H. Walker. 1993. An African savanna: Synthesis of the Nylsvley study. Cambridge University Press, UK.

Seastedt, T.R., J.M. Briggs, and D.J. Gibson. 1991. Controls of nitrogen limitations in tallgrass prairie. Oecologia 87:72-79.

Senock, R.S., W.B. Sisson, and G.B. Donart. 1991. Compensatory photosynthesis of *Sporobolus flexuosus* (Thurb.) Rydb. following simulated herbivory in the northern Chihuahuan desert. Bot. Gaz. 152:275-281.

Smit, G.N. 1999. Guide to the Acacias of South Africa. Briza Publications, Pretoria.

Smith, D.A. and E.M. Schmutz. 1975. Vegetative changes on protected versus grazed desert grassland ranges in Arizona. J. Range. Manage. 28:453-458.

Snyman, H.A. 1998. Dynamics and sustainable utilization of rangeland ecosystems in semi-arid climates of southern Africa. J. Arid Environ. 39:645-666.

Snyman, H.A. 2002. Short-term response of rangeland botanical composition and productivity to fertilization (N and P) in a semi-arid climate of South Africa. J. Arid Environ. 50:167-183.

Stark, S., R. Strommer and J. Tuomi. 2002. Reindeer grazing and soil microbial processes in two suboceanic and two subcontinental tundra heaths. Oikos 97:69-78.

StatSoft, Inc. 2004. STATISTICA for Windows [Computer program manual]. Tulsa, OK: StatSoft, Inc, USA.

Tainton, M.M., R.H. Groves, and R. Nash. 1977. Time of mowing and burning veld short-term effects on production and tiller development. Proc. J. Grassl. Soc. Sth. Afr. 12:59-94.

Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecol. Monogr. 57:189-214.

Trollope, W.S.W. 1982. Ecological effects of fire in South African savannas. p. 292-306. *In:* B.J. Huntley and B.H. Walker (eds), Ecology of tropical savannas. Springer-Verlag, Berlin.

Trollope, W.S.W. 1987. Effects of season burning on grass recovery in the False Thornveld of the Eastern Cape. J. Grassl. Soc. Sth. Afr. 4:74-77.

Trollope, W.S.W. 1999. Veld burning: Fire behaviour. p. 218-228. *In:* N.M. Tainton (ed.) Veld management in South Africa. University of Natal Press, Pietermaritzburg.

Turner, C.L., T.R. Seastedt, and M.I. Dyer. 1993. Maximization of aboveground grassland production: the role of defoliation frequency, intensity, and history. Ecol. Appl. 3:175-186.

Ulyatt, M.J. 1973. The feeding value of herbage. p. 131-178. *In:* G.W. Butler and R.W. Bailey, (eds). Chemistry and Biochemistry of herbage Vol. 3. Academic Press, London.

Vallentine, J.F. 2001. Grazing management. Academic Press, San Diego.

Van de Vijver, C.A.D.M., P. Poot, and H.H.T. Prins. 1999. Causes of increased nutrient concentrations in post-fire regrowth in an East African savanna. Plant Soil 214:173-185.

Van Oudtshoorn, F. 1999. Guide to grasses of southern Africa. Briza Publications, South africa.

Varnamkhasti, A.S., D.G. Milchunas, W.K. Luaenroth, and H. Goetz. 1995. Production and rain use efficiency in short-grass steppe: grazing history, defoliation and water resource. J. Veg. Sci. 6:787-796.

Walker, B.H. and W.T. Knoop. 1987. The responses of the herbaceous layer in a dystrophic *Burkea african* savanna to increased levels of nitrogen, phosphate and potassium. J. Grassl. Soc. Sth. Afr. 4:31-34.

Wallace, L.L., S.J. McNaughton, and M.B. Coughenour. 1984. Compensatory photosynthetic responses of three African graminoids to different fertilization, watering and clipping regimes. Bot. Gaz. 145:151-156.

Wilman, D. 1975. Nitrogen and Italian ryegrass. 2. Growth up to 14 weeks: nitrogen, phosphorus and potassium content and yield. J. Br. Grassl. Soc. 30:243-249.

Willms, W.D., Dormaar, W.J.F, B.W. Adams and H.E. Douwes. 2002. Response of the mixed prairie to protection from grazing. J. Range Manage. 55:210-216.

Wilson, J.R. 1982. Environmental and nutritional factors affecting herbage quality. p. 111-131. *In:* J.B. Hacker (ed.), Nutritional limits to animal production from pastures. Commonwealth Agriculture Bureaux: Farnham Royal, UK.

Wilson, J.R. and J.D. Minson. 1980. Prospects for improving the digestibility and intake of tropical grasses. Trop. Grassl. 4:253-259.

Wolfson, M.M. and N.M. Tainton. 1999. The morphology and physiology of the major forage plants. p. 54-79. *In:* N.M. Tainton (ed) Veld management in South Africa. University of Natal Press, Pietermaritzburg.

Zacharias, P.K.J. 1986. The use of the cellulase digestion procedure for indexing the dry matter digestibility of forage. J. Grassl. Soc. Sth. Afr. 3:117-121.

Chapter 3

Determining spatial and temporal variability in quantity and quality of vegetation for estimating the predictable sustainable stocking rate in the semi-arid savanna

Abstract

This study assessed the importance of spatial and temporal variation in plant quality and quantity for determining sustainable stocking rates in game, commercial and communal ranches in semi-arid savanna of the Northern Cape Province, South Africa in wet and dry seasons over a two-year period. We focused on variation in plant biomass, phosphorus (P), crude protein (CP) concentrations and dry matter digestibility as parameters most likely to affect sustainable stocking rates. Habitat type had greater effects on plant quality, plant biomass and species composition than management type. The commercially-managed area had the highest tree density in the rocky habitat and lower plant quality than other management types. All of these features indicate that land degradation is occurring in spite of rotational grazing and lower stocking density than on the communal ranch. We recommend that commercial ranchers should introduce a greater variety of stock and/or game to reduce selective grazing of certain plant species. Quality measures (CP and P) gave more conservative predictions of stocking density than biomass. In this region of the Northern Cape, seasonally-inundated pan habitats are particularly valuable in spite of low standing crop because they have the highest year-round quality. Contrastingly, ranchers should only lightly stock open savanna habitats in spite of high standing biomass because they have low vegetation quality and may be particularly susceptible to degradation and invasion by poisonous and unpalatable plants.

Keywords: plant quality, plant biomass, crude protein, phosphorus, plant species, management type, habitat type, stocking density

Submitted as:

Khanyisile R. Mbatha and David Ward, Determining spatial and temporal variability in quantity and quality of vegetation for estimating the predictable sustainable stocking rate in the semi-arid savanna. *African Journal of Forage and Range Science*

Introduction

Rainfall and, consequently, plant production in the semi-arid savanna of southern Africa is highly variable in space and time (Smith and Schutz 1975, Barnes and McNeil 1978, Walker and Knoop 1987, Ward *et al*. 2004). Large, unpredictable fluctuations in plant production and changes in plant cover and plant species ultimately result in negative effects on animal production. Ranchers attempting to maximise economic returns inevitably maximise short-term stocking rates at the expense of long-term sustainability of the vegetation. As a consequence, land degradation is a frequent outcome in these areas (Düvel 1995, Hoffman and Ashwell 2001).

Many South African ranchers are affected by an ongoing degradation of natural grazing resources that manifests itself in soil erosion, low land fertility, poor livestock performance, unproductive areas and bush encroachment (Düvel 1995, Hoffman and Ashwell 2001). These ranchers realise that land degradation can only be avoided by adopting a long-term view of stocking rate. However, the inherent spatio-temporal variability in plant production in semi-arid environments makes calculation of optimal long-term stocking rates extremely difficult (see e.g. Ward *et al*. 2004). Results from North America, Africa and Australia have shown that stocking rate, rather than grazing system has the greatest effect on vegetation, animal production and financial returns (Morris *et al.*1999, Hardy *et al.* 1999, Tainton *et al.* 1999, Holechek *et al*. 2004). A conservative stocking rate generally involves a harvest coefficient (=% total forage resources assigned to grazing animals for consumption in a ranch) of about 35% for semi-arid and arid regions (Holecheck *et al*. 2004). The technique of calculating stocking rate using harvest coefficient is more efficient than using total standing crop because it results in high levels of standing crop throughout the year and increased perennial grass presence. Lack of vegetation residue in the ranch may result in soil erosion, less plant regrowth activity, poor diet quality and less wildlife habitat diversity (McCalla *et al*. 1984). This problem is especially acute if the area is bush encroached because increased tree density reduces the space available for grasses and herbs, consequently reducing forage available for grazers (Archer *et al.* 1995). This, in turn, leads to reduced plant quality and quantity and, eventually, to poor animal performance and productivity.

Productivity of savannas is determined not only by plant available biomass but depends in large part on the amounts of nutrients stored in various parts such as vegetation, soil, and animal biomass, and on the interactions among these parts (Ruess 1987, Skarpe 1990). The nutritional value of forage is the most important factor influencing animal performance (Ulyatt 1973, Bransby 1981, Freer 1981). Forage quality on natural grazing lands of semi-arid regions is highly variable both spatially and temporally (Robbins 1993, Caughley and Sinclair 1994, van Soest 1994). This causes seasonal changes in diet quality, accessibility and availability (Kiringe *et al*. 1999). However, plant minerals depend on a number of factors, including soil, plant species, vegetation type, management type, stage of plant growth, plant biomass as well as climate (Reid and Horvath 1980, McDowell 1996). Most naturally-occurring mineral deficiencies in mammalian herbivores are associated with specific regions and are directly related to soil characteristics. According to Roberts (1987), soil and topography can cause constraints on plant biomass and can have effects on nutrition and growth of plants. Moreover, soil is a major source of environmental variation that determines grassland plant species composition and quality (Noy-Meir 1995). Grazing animals can obtain certain amounts of minerals from water and soil ingestion, although plants are the most important dietary source of minerals (McDowell 1996).

For animals grazing in natural veld, phosphorus (P) is the mineral most likely to be deficient (McDowell 1996). South African soil is known to lack P (Du Toit *et al.* 1940, Schmidt and Snyman 2002). Also, crude protein (CP) is a major limiting factor in mammalian herbivores as plants offer low concentrations of protein (Milford and Minson 1965). Low plant CP levels, as well as increased levels of lignification of forage, result in low forage intake, eventually reducing total nutrient intake. As plants grow there is a greater need for fibrous tissue, thereby resulting in reduced digestibility (McDonald *et al.* 1996).

The objective of this study was to assess the importance of spatial and temporal variation in plant quality and quantity for determining sustainable stocking rates in game, commercial and communal ranches in semi-arid savanna of the Northern Cape Province, South Africa in wet and dry seasons over a two-year period. We focused on variations in plant biomass, P, CP levels and dry matter digestibility as parameters most likely to affect sustainable stocking rates. We set out to compare the effects of the three management types on vegetation biomass and quality, while controlling for differences in soil types. We used a single large estate with game, commercial and communal management types to reduce possible confounding effects introduced by environmental differences and history of land use.

Materials and methods

Study area

This study was conducted on Pniel Estates (25 000ha) situated in the Northern Cape Province, South Africa, located at 28º 36' S, 24º 32' E, 1 124m. Pniel Estates consists of a game ranch (10 000ha), a commercial cattle ranch (12 000ha) and a communal ranch (3 000ha). The close proximity of these ranches and the similarity in soil type facilitate comparison of the impacts of game, communal and commercial management on forage quality and quantity in semi-arid savanna. Mean stocking density on the game area was 10.96ha SLU^{-1}, on the communal ranch was 9.37ha LSU^{-1} and 16ha LSU^{-1} on the commercially-managed area (Smet and Ward 2005).
The vegetation type in this semi-arid savanna is known as Kalahari Thornveld (Acocks 1988) or Kimberley Thorn Bushveld (Low and Rebelo 1998). In all management types, there is a rocky habitat type, which is characterized by andesite rocks, short grasses, forbs and shrubs (mostly *Acacia mellifera)* and its soil type is mainly sandy loam. *Acacia. mellifera* is encroaching (Kraaij and Ward in press), and seriously reduces grass available to mammalian herbivores and minimizes free movement of ungulates due to its thorniness. Open savanna habitat type is also found in all management types. *Acacia erioloba* trees form most of the overstory and the understory consists of a wide diversity of grasses and herbaceous plants in sandy soil. Usually under *A. erioloba,* there are shrubs such as *A. tortilis, Lebeckia linearifolia, Grewia flava, Lycium bosciifolium, L. hirsutum, Tarchonanthus camphoratus* and *Ziziphus mucronata.* The game ranch has two more habitat types that do not exist in the other management types, namely shrub and pan (=shallow ephemeral water bodies) habitat types. Mostly *T. camphoratus, G. flava*, grasses and herbaceous plants in sandy clay soil characterize shrubby habitat. Pan habitat has vegetation that differs in species and life form composition from the surrounding savanna (Parris and

Child 1973) as all plant species are dwarfed. This habitat is seasonally inundated and has dark clay soil. In our study area, the dominant grass species in the clay-pan habitat, *Eragrostis lehmanniana, E. obtusa and Cynodon dactylon,* are perennials.

Climate and soil

The study area forms part of the summer rainfall area in South Africa. The mean annual rainfall to nearest town, Barkly West, is 388mm; rainfall among years is extremely variable (C.V. = 39%) (Kraaij 2002, Kraaij and Ward in press). Most rain occurs in the form of thunderstorms between January and March, with very little rain between May and October. The temperature varies between -8°C and 41°C, with a mean of 19°C (Low and Rebelo 1998). Daily maximum temperatures exceed 30°C in summer, while for the remainder of the year the days are warm, and the nights in winter are very cold (Van Riet and Louw 1999). During the study period from 2001 to 2004, the annual rainfall was 29% above mean rainfall in 2000/2001; 21% below average in 2001/2002 and in 2002/2003 was 71% below average (severe drought) (Figure 3.1).

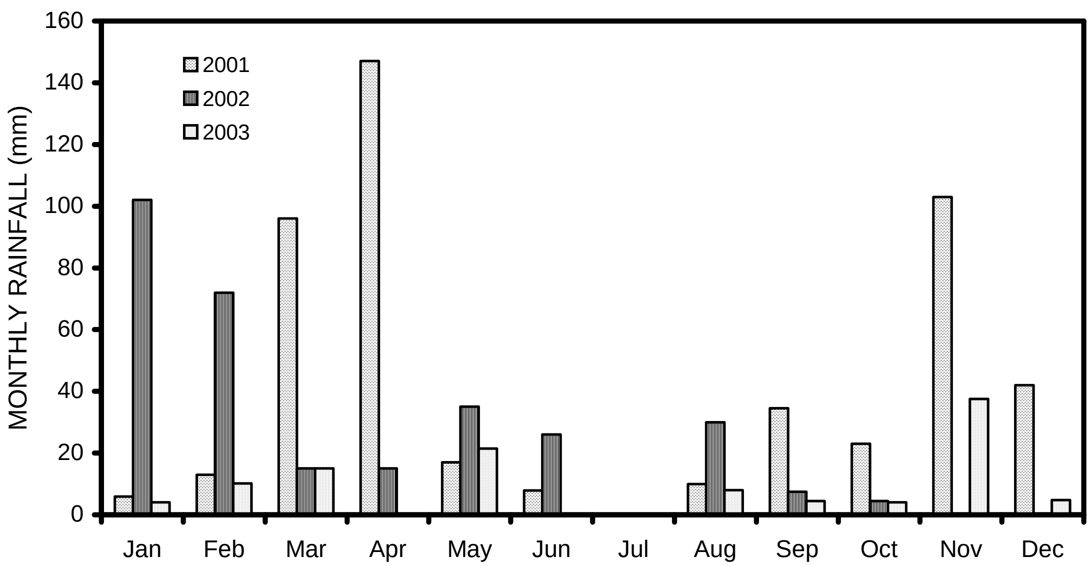

Figure 3.1: Distribution of monthly rainfall at Barkly West during the study period (2001-2003)

Most soils are leached or calcareous due to the hot dry conditions (Low and Rebelo 1998). The soils consist of a thin layer of light brown sandy loam that is underlined by either hard limestone or hard sand loam. The soil type at Pniel varies from moderately deep (0.3 – 0.6m) to deep (> 0.6m) red and yellow sands (Hutton, Clovelly and Kimberley soil forms) to shallow (< 0.3m) and stony (Mispah, Prieska and Glenrosa soil forms) (Bezuidenhout 1995). Sandy soils can be up to 8m deep and consist of 95% quartz (Van Riet and Louw 1999).

Field experiments

Soil sampling

Two randomly-selected soil samples were collected and then combined to form one composite soil sample for each plot. Core soil samples were collected from the top 20cm of soil after the surface-plant debris and stones were removed.

Plant species diversity, evenness, composition and biomass

Unfenced plots were randomly-selected in different management and habitat types (Table 3.1). All plots were 5m x 5m except plots in pan habitat that were 3m x 3m. We used a Global Positioning System and poles to mark all plots. Data were collected in wet (January) and dry (September) seasons from January 2002 to January 2004. We could not collect data in the early dry season because this season coincides with the hunting season.

Table 3.1: Total number of experimental plots in each management and habitat types

Habitats	Game management	Communal management	Commercial management
Open savanna	6	6	8
Rocky	6	6	6
Pan	6		
Shrubby	6		

The point-frequency frame (also called a "Levy bridge") is a quick and effective method of estimating plant height, species composition and percentage cover (Mueller-Dombois and Ellenberg 1974). The point-frequency frame is placed with its legs over the vegetation to be measured and pins are lowered vertically one after the other. The point at which the pin touches the vegetation is recorded as the height of the plant species. Ten placements of the pin result in 100 sample points. The mean of each frame replacement will be taken as a single data point to avoid pseudo-replication. The Levy-bridge was randomly-positioned ten times in each of the shrubby, rocky and open savanna plots and five times in the pan habitat plots to measure grass height in each plot. While measuring height, all plant species observed were recorded in all habitat and management types. Species richness, Shannon diversity index ($\log_2$) (Magurran 1988) and species composition were compared among plots of habitat and management types. We used Detrended Correspondence Analysis (DCA) in MVSP (Kovach 1999) to analyze differences in plant species composition among habitat and management types. DCA is an improved multivariate eigenvector technique based on reciprocal averaging, but correcting its main faults (Ward *et al.* 2004). Significance of differences in DCA values between habitat and management types was tested by comparing Euclidean distances among all pairs of plots on the first two DCA axes. The mean Euclidean distances values of similar plots (e.g. rocky vs. rocky; communal vs. communal) were compared with mean Euclidean distances between dissimilar plots (rocky vs. open savanna; communal vs. commercial). If the habitat or management types differ in composition on these two axes then mean Euclidean distances between similar plots should be smaller than between dissimilar plots. Conversely, if habitat or management types do not differ in species composition, there should be no significant difference between mean Euclidean distances for similar and dissimilar plots. Bootstrapping was used to compare Euclidean distances (Manly 1997) because they do not conform to a normal distribution (see e.g. Ward *et al.* 1999); specifically, we compared the actual mean difference between similar and dissimilar plots with mean differences from 1000 random re-arrangements of

DCA values among plots. If the actual difference is greater than the random difference at least 950 times out of 1000, the difference between habitat or management types is statistically significant at $\alpha = 0.05$. We note that this procedure is analogous to the ANOSIM procedure performed in the PRIMER statistical package (Ludwig and Reynolds 1988).

To convert mean plant height values to biomass, we regressed plant height values on biomass assessed from a sub-set of samples in each plot. A 1m x 1m grid was placed over the Levy-bridge in each plot and vegetation within the grid was clipped as close to the ground as possible. This was repeated three times in each plot except for plots in pan habitat type where grid was placed twice and vegetation was also clipped as close to ground as possible. Aboveground biomass was calculated as the sum of the biomass of live and green plants as well as standing dead plant material. Biomass production or yield of CP and P was calculated for each plot by multiplying percentage concentration and biomass. Clipped plant samples were oven dried at 60ºC to constant mass and then weighed to estimate plant dry weight. All plant samples were ground through a 1mm mesh screen, and stored in sealed plastic containers at room temperature pending analysis. The samples were later analyzed for CP, P and dry matter digestibility.

Tree density

The T-square sampling technique was used to estimate tree density (first described by Besag and Gleaves 1973). Random points were located in each plot of the study area and two distances were measured at each random point. From a first random point a distance (*D*) was measured to the nearest tree (*T).* An imaginary line was laid at right angles to the line joining *D* and *T.* Thereafter, a second distance (*P*) was measured from the tree (*T*) to its nearest neighbouring tree on the opposite side of the imaginary line that is perpendicular to the line TD. The angle *DTP* was always more than 90°*.* The T-square sampling method gives reliable density measurements even if the tree distribution is not random (Greenwood 1996).

There were two randomly-located points in each plot, resulting in 12 tree density estimates in the rocky habitat type as well as 12 in the open savanna habitat type of the communally-managed area. In the commercially-managed area, 22 points were randomly located in the rocky and open savanna habitat types, making a total of 44 tree density estimates in the commercial ranch. Twelve points were randomly located in rocky, open savanna, and shrubby habitat types, totalling 36 tree density estimates in the game ranch. The total number of randomly-placed points in each management type was determined according to the size of the area where a particular management type is applied. Tree density was not estimated in the pan habitat type because it has near zero density of trees. The clumping and dispersion of trees was measured by a technique mentioned by Greenwood (1996).

Chemical analyses

Soil characteristics

All the soil samples were air dried and sieved through a 2mm mesh size and stored in a cool place pending analysis. These samples were tested for the presence of inorganic carbon in the form of $CaCO_3$ by adding concentrated hydrochloric acid according to the method of Nelson and Sommers (1982). Thereafter, soil samples were analysed for pH, conductivity and percentage organic carbon. Soil pH was measured by mixing the soil sample with a water solution in a ratio of 1:5 soil and water (according to Brinkley and Vitousek 1996) using a Corning pH meter 430. Soil conductivity was determined in a 1:5 soil and water ratio saturation extract (Rhoades 1982) using a Corning conductivity meter 441. Organic carbon content was determined using the Walkley-Black method (Nelson and Sommers 1982). This method was used to avoid misinterpretation of organic carbon due to the presence of inorganic carbon in the form of carbonate in calcareous soil. Soil total nitrogen was measured using Dumas's total combustion method (Bremner 1996) with a LECO FP-528 nitrogen analyser. Available P was analysed using the Bray II method (Bray and Kurtz 1945). Water-holding capacity of soil was determined through comparisons of the volume of water contained in each soil type at saturation level (Rhoades 1982).

Nutritional characteristics of plants

Concentration of plant CP was determined using a standard Kjeldahl technique (AOAC 1990). Plant phosphorus concentrations were analyzed spectrophotometrically according to the micro technique of the AOAC (1990). The dry matter digestibility of grass species was indexed by the *in vitro* digestible dry matter method of Zacharias (1986) because this technique incorporates concentrations, ratios and structures of forage constituents in an index of potential for breakdown by rumen microbial populations (Milchunas *et al.* 1995).

Stocking rate

Stocking rate was calculated in terms of percentage of allowable forage use according to grass biomass available in the following way: Firstly, the total area occupied by trees was estimated for each management type and it was subtracted from the total area of the concerned management type. The total production of grass and forbs on a dry matter basis in each management type was estimated. A harvest coefficient (HC) of 35% (see Introduction) was selected because our study area is in a semi-arid region (Holecheck *et al.* 2004). Total number of animals was estimated using the mean body mass of a cow (450kg) and assuming that its daily consumption is approximately 3% of its body mass (Ward *et al*. 2004). Thereafter, the number of days per year was divided into wet and dry seasons. Therefore, total stocking rate of cattle per management type in the wet season was estimated by: (AM –TD)* HC *GB /(3% DC *WD) and in the dry season by: (AM –TD) * HC *GB / 3% DC *DD, where AM = total area of each management type, DC = daily consumption, DD = number of dry days per annum, GB = grass biomass per season, HC = harvest coefficient, TD = area occupied by tree density, and WD = number of wet days per annum. Stocking rate was also estimated using CP (g/day) and P (g/day) as indicated by NRC (1996) using the above-mentioned formula. Instead of 3% of its body mass, daily required CP and P for a cow weighing 450 kg based on NRC (1996) estimates were used.

Statistical analyses

Normality of data distribution was confirmed by the Shapiro-Wilk's W test (Shapiro *et al*. 1968, StatSoft 2002). Differences among management and habitat types were measured by randomized block ANOVA comparison. Type III sums of squares were used for ANOVA (Milliken and Johnson 1992). Where necessary, data were transformed to meet the requirements of parametric analyses. Scheffe *post hoc* comparisons of means were performed on plant biomass, height, CP, P and all soil chemical characteristics of different management and habitat types. Pearson product-moment correlation analyses were used for comparisons of plant height and plant biomass, plant biomass and plant CP, plant biomass and P and among soil characteristics.

Results

Soil characteristics

Organic carbon content

Organic carbon concentration in the soil was significantly different ($F_{3, 46} = 12.41$, $P < 0.001$) among habitat types (Table 3.2). Organic carbon did not differ significantly among management types ($F_{2, 47,} = 2.27$, $P = 0.11$; Table 3.3). The pan habitat type had significantly more soil organic carbon content than open savanna, rocky and shrubby habitat types (*post hoc* tests, $P < 0.05$).

Nitrogen (N) content

There was a significant difference among habitat types ($F_{3. 47} = 4.42$, $P = 0.01$) in soil N level (Table 3.2). Similarly, management type had a significant effect ($F_{3, 46} = 3.18$ $P = 0.04$) on soil N (Table 3.3). According to *post hoc* tests, the game management type had significantly higher levels of soil N than the other management types.

Phosphorus (P) content

A significant influence ($F_{2, 47} = 3.78$, $P = 0.03$) of management type on soil P levels was observed (Table 3.3). Similarly, soil P concentration differed significantly ($F_{3, 46} = 49.89$, $P < 0.001$) among habitat types (Table 3.2). Pan habitat type had significantly higher soil P levels than rocky, open savanna and shrubby habitats (*post hoc* tests, $P < 0.05$).

pH level

There was a significant difference ($F_{3, 46} = 8.20$, $P < 0.001$) in soil pH levels among different habitat types (Table 3.2). Soil pH levels did not differ significantly ($F_{2, 47} = 0.65$, $P = 0.94$) among management types (Table 3.3). Results from Scheffe *post hoc* tests showed that soil pH levels of pan habitat were significantly higher than in open savanna, rocky and shrubby habitat types.

Water-holding capacity

Management type had no influence on water-holding capacity of the soil ($F_{2, 47} = 3.41$, $P = 0.42$; Table 3.3). In contrast, habitat types showed significant differences ($F_{3, 46} = 57.11$, $P < 0.001$) in water-holding capacity (Table 3.2). Results from Scheffe *post hoc* tests showed that the pan habitat type had greater water-holding capacity than open savanna, rocky and shrubby habitat types. Similarly, water-holding capacity in rocky and shrubby habitat types was significantly higher than in open savanna.

Conductivity

Soil conductivity levels showed no significant difference ($F_{2, 47} = 2.13$, $P = 0.13$) among management types (Table 3.3). In contrast, habitat types differed significantly ($F_{3, 46} = 10.48$, $P < 0.001$) in soil conductivity (Table 3.2). Pan habitat type had significantly higher levels of soil conductivity than open savanna, shrubby and rocky habitat types (*post hoc* tests $P < 0.05$). Nitrogen, P, pH, water-holding capacity and conductivity levels of soil showed a strong significantly positive correlation with organic carbon levels (Table 3.4).

Plant species diversity, evenness and composition

There was a significant effect ($F_{3, 73} = 4.14$, $P = 0.009$; $F_{3, 73} = 4.15$, $P = 0.009$) of habitat type on species diversity and evenness respectively over the study period. Shrubby habitat had greater species diversity than other habitat types (*post hoc* tests $P < 0.05$). Similarly, species diversity differed significantly ($F_{2, 74} = 5.44$, $P = 0.006$) among management types (communal = 0.8 ± 0.02; game = 0.72 ± 0.001 and commercial 0.73 ± 0.02; mean ± SE). According to Scheffe *post hoc* tests, the communal management type had more diverse plant species than game and commercial management types. In contrast, the effects of management types were similar ($F_{3, 74} = 1.70$, $P = 0.19$) on species evenness. The most unpalatable species were frequently observed in the open savanna habitat and the palatable plant species were in shrubby habitat type (Table 3.5). The game ranch had the least unpalatable plant species and the communally-managed area had the greater number of unpalatable plant species (Table 3.6).

The eigenvalues for the Detrended Correspondence Analysis (DCA) of species composition data for the last sampling period (January 2004) were 0.545 and 0.333 for Axis 1 and Axis 2, respectively. These axes explained 10.8 % and 6.6% of the variance in species composition, respectively. A significant difference in Euclidean distances (P < 0.001, significance determined by 1000 bootstrap resamples of the data – see *Methods*) among habitat types was found (Figure 3.1). This difference in species composition scores among habitat types was found on both Axis 1 (P = 0.022) and Axis 2 (P = 0.029). The most obvious differences in species composition were between rocky and open savanna habitats on DCA axis 1, with the shrubby habitat occurring in an intermediate position on this axis. No significant difference in species composition was found between management types on either Axis 1 (P = 0.066) or Axis 2 (P = 0.676).

Table 3.2: Mean (± SE) soil organic carbon, nitrogen, phosphorus, pH, water-holding capacity and conductivity levels in different habitat types on Pniel Estates

Parameter	Habitat	Mean (± SE)
Organic carbon (%)	Savanna	0.62 ± 0.05
	Rocky	0.76 ± 0.05
	Shrubby	0.72 ± 0.11
	Pan	1.27 ± 0.10
Nitrogen (%)	Savanna	0.05 ± 0.003
	Rocky	0.06 ± 0.003
	Shrubby	0.03 ± 0.007
	Pan	0.06 ± 0.006
Phosphorus (mg/kg)	Savanna	4.01 ± 3.74
	Rocky	8.02 ± 6.47
	Shrubby	30.78 ± 6.39
	Pan	90.85 ± 7.56
pH	Savanna	5.60 ± 0.11
	Rocky	5.76 ± 0.11
	Shrubby	5.58 ± 0.19
	Pan	6.69 ± 0.21
Water holding capacity (%)	Savanna	29.11 ± 0.71
	Rocky	34.43 ± 0.74
	Shrubby	35.71 ± 1.29
	Pan	48.25 ± 1.29
Conductivity (µS/cm)	Savanna	37.36 ± 5.20
	Rocky	46.01 ± 5.48
	Shrubby	51.02 ± 9.49
	Pan	97.52 ± 9.49

Table 3.3: Effects of management type on soil organic carbon, nitrogen, phosphorus, pH, water-holding capacity and conductivity levels (mean ± SE) on Pniel Estates

Parameter	Management	Mean ± SE
Organic carbon (%)	Communal	0.68 ± 0.081
	Game	0.86 ± 0.055
	Commercial	0.67 ± 0.065
Nitrogen (%)	Communal	0.04 ± 0.001
	Game	0.06 ± 0.003
	Commercial	0.05 ± 0.005
Phosphorus (mg/kg)	Communal	5.98 ± 8.112
	Game	29.60 ± 5.51
	Commercial	5.64 ± 6.44
pH	Communal	5.81 ± 0.12
	Game	5.78 ± 0.13
	Commercial	5.78 ± 0.15
Water- holding capacity (%)	Communal	31.39 ± 1.7
	Game	36.54 ± 1.29
	Commercial	32.30 ± 1.70
Conductivity (µS/cm)	Communal	48.99 ± 8.46
	Game	56.75 ± 5.84
	Commercial	36.89 ± 7.64

Table 3.4: Correlation coefficients (r) and significance (**bold**) of these correlations (p) (N=50) between phosphorus (P), nitrogen (N), organic carbon (Organic C), water- holding capacity (H_2O holding capacity), pH and conductivity levels of soil on Pniel Estates

Variables	P (mg/kg)	N (%)	Organic C (%)	H_2O holding capacity (%)	pH level
Nitrogen (%)	r = 0.024				
	p = 0.861				
Organic carbon (%)	**r = 0.65**	**r = 0.37**			
	p < 0.001	**p = 0.005**			
Water-holding capacity (%)	**r = 0.75**	r = 0.09	**r = 0.69**		
	p < 0.001	p = 0.50	**p < 0.001**		
pH	**r = 0.55**	r = 0.06	**r = 0.53**	**r = 0.65**	
	p < 0.001	p = 0.66	**p < 0.001**	**p < 0.001**	
Conductivity (µS/cm)	**r = 0.55**	r = -0.12	**r = 0.50**	**r = 0.68**	**r = 0.74**
	p < 0.001	p = 0.37	**p < 0.001**	**p < 0.001**	**p < 0.001**

Table 3.5: Mean ± SE of the most unpalatable species densities (number of species m^{-2}) in open savanna, rocky, pan and shrubby habitats on Pniel Estates

Species	Open savanna	Rocky	Pan
Barleria rigida	4.11 ± 0.15	3.0 ± 0.12	
Boophane disticha	2.2 ± 0.26		
Chrysocoma ciliata	7 ± 0.26		
Chrysocoma obtusata	3 ± 0.01	5 ± 0.43	
Crinum foetidum	4.55 ± 0.22		
Elephantorrhiza elephantine	3.67 ± 0.25		
Geigeria filifolia	1	2.5 ± 0.42	3.01 ± 0.05
Geigeria ornativa	4.78 ± 0.08	13.33 ± 0.42	2.54 ± 0.22
Gnidia polycephala	9.78 ± 0.98		
Helichrysum argyrosphaerum	4.33 ± 0.35	3.33 ± 1.09	
Lindneria clavata	4.5 ± 0.42		
Selago dinteri	4 ± 0.25	20.3 ± 0.44	3.2 ± 0.12

Table 3.6: The most available unpalatable species densities (number of species m^{-2}, mean $\pm$ SE) on game, communal and commercial ranches on Pniel Estates

Species	Commercial	Communal	Game
Barleria rigida	0	9 ± 0.01	0
Boophane disticha	4 ± 0.73	4.37 ± 0.17	0
Chrysocoma ciliata	3.5 ± 0.70	1.33 ± 0.25	0
Chrysocoma obtusata	10 ± 0.33	8.11 ± 0.14	7.5 ± 0.33
Crinum foetidum	3 ± 0.12	6 ± 1.02	3 ± 0.001
Elephantorrhiza elephantine	5.25 ± 0.38	6.25 ± 0.59	2 ± 0.001
Geigeria ornativa	0	3.67 ± 0.25	0
Geigeria filifolia	0	1.5 ± 0.11	3 ± 0.001
Gnidia polycephala	3.4 ± 0.01	9.42 ± 0.42	3 ± 0.001
Helichrysum argyrosphaerum	11.25 ± 0.80	5.67 ± 0.72	2.67 ± 0.21
Lindneria clavata	0	4.5 ± 0.42	0
Selago dinteri	7.17 ± 0.22	24.88 ± 0.55	7 ± 0.21

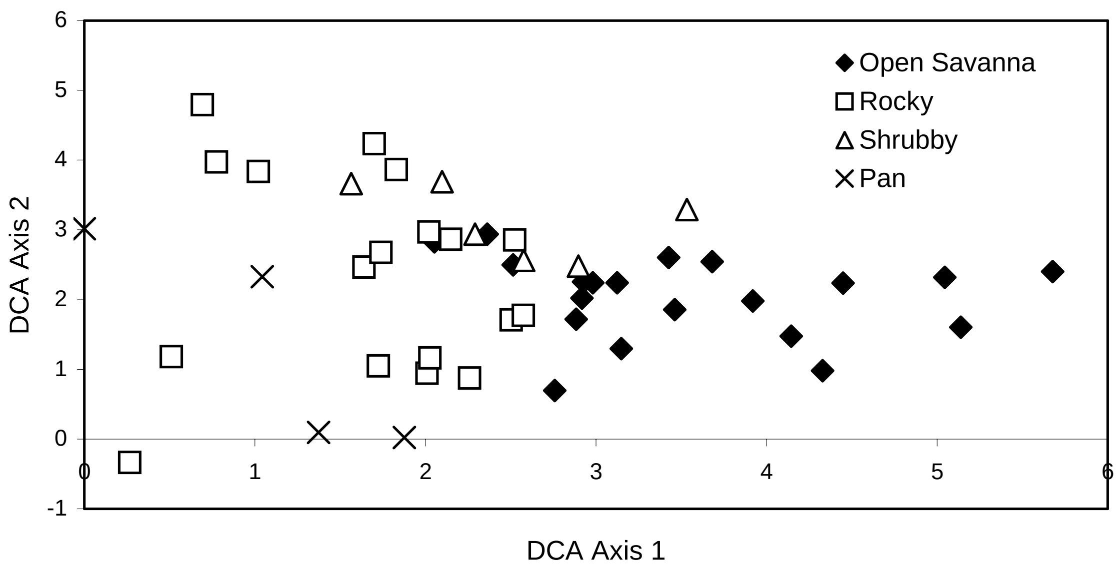

Figure 3.2: Differences in species composition during 2004 wet season among habitat types as determined by Detrended Correspondence Analysis (DECORANA)

Tree density

Trees in all open savanna habitats were regularly dispersed, according to the technique of Besag and Gleaves (1973). In the open savanna of the game area, there was a mean ± S.E. of 50 ± 14.75 trees ha^{-1}, while there were 70 ± 17.57 trees ha^{-1} in the open savanna of the commercial ranch. The open savanna of the communal ranch had a more clumped tree distribution and a higher number of trees (87 ± 12.60 trees ha^{-1}) than other open savanna habitat types. The rocky habitat type was observed to have more clumped and a higher number of trees per hectare than the open savanna. The rocky habitat of the commercially-managed area had the highest number of trees (1190 ± 10.33 trees ha^{-1}). In the rocky habitat of the communal ranch, there were 574 ± 6.35 trees/ha. In the rocky habitat of the game area, there were 372 ± 44.75 trees ha^{-1} and trees were regularly dispersed compared to communal and commercial ranches. The mean number of trees observed in the shrubby area of the game management type was 313 ± 5.45 $ha^{-1}$and their distribution was clumped.

Plant biomass

Management type significantly affected plant biomass ($F_{2, 47}$ = 11.827, P < 0.001; $F_{2, 42}$ = 4.24, P = 0.02; $F_{2, 46}$ = 4.639, P = 0.014 and $F_{2,470}$ = 5.06, P = 0.009) in the 2002 wet, 2002 dry, 2003 wet and 2004 wet seasons, respectively (Table 3.7). From *post hoc* tests, in the wet season of 2002, plant biomass was lower in the communal management type than in the commercial and game ranches. The commercial management type had a higher plant biomass than in the communally-managed area in both the dry season of 2002 and the wet season of 2003 (*post hoc* tests P < 0.05). In the 2003 dry season, management type had a non-significant influence ($F_{2, 45}$ = 2.48, P = 0.09) on plant biomass, which was a year when rainfall was 71% less than the long-term mean annual rainfall (Table 3.7). From *post hoc* tests, in the wet season of 2002, plant biomass was lower in the communal ranch than in the commercial and game management types. The commercial ranch had a higher biomass than in the communal ranch in both the dry season of 2002 and the wet season of 2003 (*post hoc* tests P < 0.05).

Habitat type showed significant effects ($F_{3, 47}$ = 5.21, P = 0.003; $F_{3, 46}$ = 8.39, P < 0.001 and $F_{3, 47}$ = 4.84, P = 0.005) on plant biomass in the wet seasons of 2002, 2003 and 2004, respectively (Table 3.8). The plant biomass of the open savanna habitat was significantly higher than in rocky and pan habitat types in the 2002 wet season. In the wet season of 2003, open savanna demonstrated a significantly higher plant biomass than in shrubby and pan habitats. Plant biomass differed non-significantly ($F_{3, 42}$ = 0.14, P = 0.93 and $F_{3, 44}$ =1.89, P = 0.14) among habitat types in the dry seasons of 2002 and 2003, respectively (Table 3.8). There was a strong positive and significant correlation between plant height and plant biomass (r = 0.6, N = 230, P < 0.001) across seasons.

Table 3.7: Mean plant biomass ($g/m^2 \pm SE$) of different management types in the wet and end of dry seasons of Pniel Estates during 2002- 2004

Year	Season	Management	Mean ± SE
2002	Wet	Game	113. 52 ± 6.29
		Communal	43.09 ± 11.23
		Commercial	95.80 ± 9.88
2002	End of dry	Game	37.45 ± 4.09
		Communal	24.88 ± 5.79
		Commercial	47.84 ± 3.36
2003	Wet	Game	30.38 ± 2.86
		Communal	21.33 ± 5.11
		Commercial	33.14 ± 4.49
2003	End of dry	Game	25.21 ± 2.81
		Communal	18.74 ± 5.01
		Commercial	29.05 ± 4.41
2004	Wet	Game	47.92 ± 3.97
		Communal	42.36 ± 7.09
		Commercial	63.90 ± 6. 23

Forage nutritional quality

Dry matter digestibility

Management and habitat types had similar effects on in vitro dry matter digestibility (range in P = 0.11 – 0.64) during the study. The mean *in vitro* dry matter digestibility in the wet seasons ranged between 48.95 – 59.91% and between 36.87 – 47.80% in the dry seasons.

Crude protein (CP) content

Significant effects ($F_{2, 47} = 3.92$, $P = 0.03$ and $F_{2, 42} = 4.24$, $P = 0.02$) of management types were observed on plant CP content of the wet and the dry seasons of 2002, respectively (Table 3.9). In the dry season of 2002, communal management types showed significantly higher plant CP levels than in the commercial management type. Management types had a non-significant effect ($F_{2, 46} = 0.389$, $P = 0.96$; $F_{2, 42} = 1.56$, $P = 0.22$ and $F_{2, 47} = 0.63$, $P = 0.54$) on plant CP levels in the wet and the dry seasons of 2003, as well as in the wet season of 2004, respectively (Table 3.9).

Table 3.8: Mean values of plant biomass (g/m^2 ± SE) among habitat types in the wet and end of dry seasons during the study period (2002-2004) on Pniel Estates

Year	Season	Habitat	Mean ± SE
2002	Wet	Open savanna	116.69 ± 6.79
		Rocky	72.21 ± 7.27
		Shrubby	83.03 ± 14.47
		Grassy pans	64.63 ± 14.47
2002	End of dry	Open savanna	36.91 ± 4.90
		Rocky	35.84 ± 5.17
		Shrubby	38.29 ± 8.95
		Grassy pans	42.37 ± 8.94
2003	Wet	Open savanna	43.12 ± 3.09
		Rocky	31.87 ± 3.31
		Shrubby	21.39 ± 6.59
		Grassy pans	16.74 ± 6.58
2003	End of dry	Open savanna	27.65 ± 3.03
		Rocky	18.89 ± 3.24
		Shrubby	26.14 ± 6.46
	Wet	Grassy pans	24.66 ± 6.46
2004		Open savanna	55.98 ± 4.28
		Rocky	42.27 ± 4.58
		Shrubby	69.15 ± 9.13
		Grassy pans	38.18 ± 9.13

Table 3.9: Mean values of plant CP and P concentrations (% ± SE) among management types during wet and dry season on Pniel Estates over two years (Jan 2002 – Jan 2004)

Year	Season	Management	CP	P
2002	Wet	Game	6.49 ± 0.29	0.09 ± 0.006
		Communal	7.09 ± 0.41	0.09 ± 0.009
		Commercial	6.91 ± 0.38	0.08 ± 0.008
2002	End of dry	Game	7.12 ± 0.24	0.10 ± 0.007
		Communal	7.07 ± 0.32	0.08 ± 0.01
		Commercial	5.58 ± 0.25	0.06 ± 0.009
2003	Wet	Game	8.91 ± 0.21	0.12 ± 0.005
		Communal	8.91 ± 0.32	0.10 ± 0.007
		Commercial	8.88 ± 0.28	0.09 ± 0.006
2003	End of dry	Game	6.95 ± 0.34	0.05 ± 0.005
		Communal	6.34 ± 0.49	0.05 ± 0.007
		Commercial	6.18 ± 0.44	0.04 ± 0.007
2004	Wet	Game	10.93 ± 0.49	0.11 ± 0.005
		Communal	11.25 ± 0.69	0.11 ± 0.008
		Commercial	10.27± 0.62	0.09 ± 0.007

Habitat types had no influence ($F_{3, 46} = 1.68$, $P = 0.19$; $F_{3, 41} = 1.27$, $P = 0.30$ and $F_{3, 45} = 1.52$, $P = 0.22$) on plant CP in the wet season and the dry season of 2002 as well as wet season of 2003, respectively (Table 3.10). In the dry season of 2003 and the wet season of 2004, habitat types showed a significant difference ($F_{3, 42} = 12.12$, $P < 0.001$ and $F_{3, 46} = 4.028$, $P = 0.01$) in plant CP, respectively (Table 3.10). Pan habitat type had significantly more plant CP content than in the open savanna, rocky and shrubby habitats in the 2003 dry season (*post hoc* tests $P < 0.05$). Similarly, in the wet season of 2004, plant CP concentration of pan habitat was significantly higher than that of rocky and shrubby habitats.

Table 3.10: Forage CP and P concentrations (mean % ± SE) among habitat types during the wet and end of dry season on Pniel Estates over two years (Jan 2002 – Jan 2004)

Year	Season	Habitat	CP	P
2002	Wet	Open savanna	6.50 ± 0.33	0.06 ± 0.005
		Rocky	6.84 ± 0.34	0.08 ± 0.005
		Shrubby	5.80 ± 0.59	0.10 ± 0.009
		Grassy pans	6.38 ± 0.59	0.14 ± 0.009
2002	End of dry	Open savanna	6.56 ± 0.23	0.07 ± 0.013
		Rocky	6.14 ± 0.25	0.10 ± 0.014
		Shrubby	6.04 ± 0.39	0.11 ± 0.02
		Grassy pans	7.58 ± 0.39	0.14 ± 0.02
2003	Wet	Open savanna	8.94 ± 0.23	0.08 ± 0.004
		Rocky	8.45 ± 0.24	0.10 ± 0.004
		Shrubby	8.46 ± 0.41	0.13 ± 0.008
		Grassy pans	10.01 ± 0.41	0.15 ± 0.008
2003	End of dry	Open savanna	6.23 ± 0.41	0.05 ± 0.003
		Rocky	6.98 ± 0.28	0.04 ± 0.004
		Shrubby	5.85 ± 0.28	0.08 ± 0.007
		Grassy pans	7.49 ± 0.61	0.10 ± 0.006
2004	Wet	Open savanna	11.16 ± 0.47	0.07 ± 0.005
		Rocky	10.21 ± 0.49	0.09 ± 0.005
		Shrubby	9.28 ± 0.86	0.11 ± 0.008
		Grassy pans	13.09 ± 0.86	0.15 ± 0.009

Phosphorus (P) content

Management types had a significant effect ($F_{3, 45}$ = 18.86, P < 0.001) on plant P content in the wet season of 2003 only (Table 3.9). According to *post hoc* tests during this wet season, game management type had significantly higher forage P content than in commercial management. Non-significant effects ($F_{2, 47}$ =1.17, P = 0.32; $F_{2, 42}$ = 0.38, P = 0.68; $F_{2, 46}$ = 0.69, P = 0.51 and F = $_{2, 47}$ = 1.19, P = 0.31) of management types on plant P levels in the 2002 wet and dry season as well as the dry season of 2003 and 2004 wet season respectively, were observed (Table 3.9).

A significant difference ($F_{3, 46}$ = 13.25, P < 0.001; $F_{3, 41}$ = 3.38, P = 0, 03; $F_{3, 46}$ = 18.86, P < 0.001; $F_{3, 45}$ = 24.41; P < 0.001 and $F_{3, 46}$ = 11.81, P < 0.001) among habitat types in plant P levels was observed during the whole study period i.e. 2002 wet and dry season, 2003 wet and dry season and the wet season of 2004, respectively (Table 3.10). According to Scheffe *post hoc* tests, plant P content of pan habitat was significantly higher than in other habitats during the whole study period.

Stocking rate

A high carrying capacity based on plant biomass, CP and P yields was predicted in the wet season of 2001/2002, when annual rainfall was about 29% more than long-term mean annual rainfall of the study area (Table 3.11). In 2002/2003, annual rainfall was 71% less than mean annual rainfall and the lowest stocking rate during the study period was also predicted (Table 3.11). In the game area, over five seasons, using P yield led to the most conservative stocking rate on two occasions. In the commercially-managed area, P yield gave the most conservative stocking rate in all seasons. In the communally-managed area, only twice did P yield give the most conservative stocking rate. Of the 15 occasions (five seasons x three management types) that stocking rate was calculated, on 12 occasions one of the two vegetation quality measures (CP and P) gave a more conservative prediction for conservative stocking density than biomass.

Table 3.11: Recommended stocking density (ha/LSU) per season based on P, CP and plant biomass yields in the different management types at Pniel Estates

Year	Season	Management	P	CP	Biomass
2002	Wet	Game	13.83 ± 8.06	12.68 ±2.12	11.79 ± 3.71
		Commercial	12.94 ± 6.25	8.86 ± 2.64	10.67± 6.87
		Communal	21.24 ± 3.94	14.43 ± 3.39	21.75 ± 5.27
2002	End of dry	Game	15.30 ± 7.25	21.02 ± 2.12	17.95 ± 2.75
		Commercial	19.01 ± 8.02	17.59 ± 3.33	10.73 ± 5.29
		Communal	18.52 ± 5.83	21.56 ± 3.58	18.91 ± 4.78
2003	Wet	Game	42.12 ± 14.55	51.68 ± 9.94	41.35 ± 9.05
		Commercial	33.51 ± 9.98	31.71 ± 4.02	30.85 ± 7.53
		Communal	33.44 ± 4.42	34.09 ± 6.78	31.21 ± 6.98
2003	End of dry	Game	37.31 ± 14.44	21.05 ± 2.76	26.67 ± 6.33
		Commercial	33.63 ± 12.94	15.18 ± 3.97	17.67 ± 7.34
		Communal	43.59 ± 4.67	25.92 ± 7.56	25.11 ± 9.24
2004	Wet	Game	27.25 ± 11.37	15.85 ± 2.26	27.94 ± 8.76
		Commercial	20.21 ± 9.10	12.55 ± 2.87	16.00 ± 5.34
		Communal	23.57 ± 4.69	17.91 ± 3.13	22.13 ± 6.59

Discussion

Soil characteristics

The pan habitat type had higher soil calcium carbonate as well as higher soil organic carbon, pH, N, P, water-holding capacity and conductivity levels than the other habitats. Britz (2004) reported similar results at a larger scale of the Kimberley Triangle (a 150 000ha conservation area that includes the present study area). A high level of organic carbon is an indication of soil organic matter and an indirect source of nutrients for plant growth and forage quality (Hatton and Smart 1984, Whitehead 2000). Soil organic matter also positively affects water-holding capacity (Barber 1984, Hatton and Smart 1984, Cresser *et al.* 1993) through its improvement of soil structure (Knoepp *et al.* 2000, Reynolds *et al.* 2002). Consequently, in this study, low soil water-holding capacity of open savanna habitat compared to other habitat types was observed, probably because its soil type is mostly sandy and has low organic matter content. Conversely, there was enhanced water-holding capacity in the pan habitat type in relation to other habitat types. The clay soil of pan habitat type with high pH and organic carbon levels resulted in improved hydrophilic characteristics of the pan habitat type. However, seasonal inundation, attendant water-logging and high salinity of pan habitat may be the cause of dwarf vegetation frequently observed there (Britz 2004).

Almost 95% of N and much of P in grassland soil occur in the soil organic matter (Whitehead 2000). In the present study, positive correlations between soil organic carbon and N as well as P concentrations were observed (Table 3.4) as was also recorded by Turner (1998) and Ward *et al.* (1998). Soil N and P elements are not directly available but are released in plant-available forms by the mineralization brought about by microbial enzymes (Whitehead 2000). When soil has greater amounts of soil organic matter, the decomposition rate is rapid, resulting in greater amounts of N and P (Whitehead 2000). Christensen (1977) observed that sandy soils tend to leach and have slow rates of decomposition, resulting in a higher potential for nutrient limitation; our findings conform to these observations. However, mineralization rate declines below soil pH 8 and soil N tends to be less available when pH falls below 5.5 to 6 (Cresser *et al.* 1993). Thus, mineralization rates were higher during our study because pH level was never above pH 8. Soil pH enhanced nutrient availability because the pan habitat type with high soil pH produced plants with high nutritive value.

Pan and rock habitat types had similar soil N content. In the rocky habitat, this may be attributed to lower levels of leaching and perhaps nutrients trapped between the rocks. Organic carbon in the rocky habitat was less than that observed in the pan habitat type. Thus, litter of leaves from shrubs and trees (rocky habitat is bush encroached - see below) with high levels of nutrients trapped between the rocks. Consequently, decomposition and mineralization rates were probably elevated, leading to a higher concentration of soil N in the rocky habitat type. More enhanced soil N in the open savanna than in shrubby habitat may be accredited to increased N levels resulting from elevated faecal and urine deposition by large number of animals grazing in it than in other habitat types. The open savanna habitat type of commercial and communal management types may have a high density of grazing animals because the rocky areas of these managements is highly bush encroached, resulting in reduced accessibility to grazing (see tree density below; Kraaij and Ward in press).

Soils of South Africa are low in P (Du Toit *et al*. 1940, Schmidt and Snyman 2002). This mineral is depleted in the arid rangelands (McDowell 1996) particularly in the sandy soils of Northern Cape (Donaldson and Kelk 1970). Phosphorus is usually the most limiting mineral (Du Toit *et al* 1940) and is predominantly important in mammalian herbivores because it has a great influence on palatability (Downing 1979). Soil that is deficient in P produces forage that is further reduced in P concentration (Vallentine 2001). Thus, P content can influence diet selection (Denton 1984, McNaughton 1990). The low levels of plant P observed in the open savanna habitat with sandy soil accords with the findings of Donaldson and Kelk (1970). Pan habitat type had higher soil P content (as well as enhanced plant P levels) than other habitat types; these observations are similar to the findings of Britz (2004). Thus, from our results, soil P level is positively correlated with plant P content (see below). Due to the palatability effect of high levels of P and improved nutrient value of forage, the pan habitat type attracted a wide diversity of grazers and mixed feeders (note: soil N was not consistently higher in the pans than in other habitat types – Table 3.1). This may suggest that soil quality plays a role in diet palatability and selection of mammalian herbivores. To support this, Heitkӧng and Owen-Smith (1998) observed that soil quality is of importance in the selection of landscape type by roans. The improved levels of P in the pan habitat resulted in the game management type having higher soil P levels than other management types. However, management type does not play a large role where soil characteristics are concerned because it had an influence only on soil N and P.

Tree density

Increased tree density reduces space available for grass and herbs consequently reducing forage available for grazers. Bush encroachment by thorny tree, *A. mellifera* causes a serious reduction in the availability of forage to livestock, especially in the rocky habitat type (Kraaij and Ward in press). *A. mellifera* cannot be easily browsed and animals cannot pass between due to its increased density and physical defences. In the rocky habitat type of the communally-managed and commercially-managed areas, tree density was high and clumped. The commercial ranch had 52% more trees/ha than the communal ranch. Thus, it seems that the commercial ranch has a greater problem with bush encroachment than the other management types. The absence of mixed feeders and browsers in the commercially-managed area may have resulted in higher levels of bush encroachment there. Goats, which are known to control bush encroachment (see e.g. du Toit 1972), have been excluded in the commercially-managed area for approximately four decades. Many residents in the communally-managed area believe that the bush encroachment in their area started when the previous managers of Pniel Estates banned people from ranching goats for a period of about 10 years. Further evidence for control of bush encroachment by browsers and mixed feeders comes from the observation that tree density in the rocky habitat of the game ranch was lower than in other management types, perhaps because of the wide diversity of foraging types (grazers, mixed feeders and browsers) among mammalian herbivores present there.

The shrubby habitat is also encroached but mostly by *Grewia flava* and *Tarchonanthus camphoratus.* Animals can easily pass between these shrubs and these shrubs can offer nutrients to animals, especially in the dry season when grass and herbaceous species are in low in nutrients. Open savanna was not encroached compared to other habitat types and open savanna of game area had the lowest number of trees/ha. This may also indicate that an area with various types of feeders is less likely to become bush encroached than an area with a single feeder. In the present study, the area with the greatest number of feeder types (game ranch) had the fewest signs of bush encroachment.

Plant species diversity, evenness and composition

The dominant perennial grass species in the open savanna habitat were *Schmidtia pappophoroides*, *Eragrostis lehmanniana, Eragrostis obtusa* and *Aristida congesta*. Moderately palatable *Pogonarthria squarrosa* was frequently observed in open savanna and is more abundant in communal and game management types and is considered an indicator of low nutrient sandy soil (Bezuidenhout 1994, van Oudtshoorn 1994). Other dominant grass species were palatable *Heteropogon contortus* and *Stipagrostis uniplumis*, and less palatable or unpalatable species were *Aristida diffusa* and *Enneapogon scoparius*. The dominant grass species in the pan habitat were *E. lehmanniana, E. obtusa* and *Cynodon dactylon.* These species are perennials and indicators of heavy grazing (van Oudtshoorn 1994). *Heteropogon contortus* was mostly observed in the rocky habitat type (see also McNaughton 1983; van Oudtshoorn 1994) and their leaves were grazed to the bottom of the sward while young (pers. obs.). *Enneapogon desvauxii, Enneapogon scoparius, A. congesta* and *E. obtusa* were also more frequently observed in rocky habitat types than in other habitats.

The dwarf shrubs with highest cover in the study area are *Pentzia incana, Leucosphaera bainesii, Asparagus* species, *Nolletia arenosa, Felicia muricata, F. filifolia, Monechma incanum, M. divaricatum* and *Chrysocoma obtusata*; some of these species (*P. incana, L. bainesii, F. muricata, M. incanum* and *M. divaricatum*) are known to be high in nutrients (Tainton 1999, van Rooyen *et al.* 2001). Other herbaceous plants frequently observed were *Indigofera* species, *Aptosimum* species, *Senna italica, Hermbstaedtia fleckii* and *Heliotropium lineare*. Pan habitat consisted mostly of arid karoo shrubs (*Pentzia* species, *Salsola* species, *F. muricata, Eriocephalus aspalathoides*) and other species such as *L. bainesii and M. incanum* that usually retain protein concentration of 7-10% through out the year (Boyazoglu 1973). The poisonous and unpalatable plant species *Geigeria filifolia, Geigeria ornativa, Gnidia polycephala, C. obtusata, Boophane distich, Ammocharis coranica, Elephantorrhiza elephantina, Selago dinteri* subsp*. pseudodinteri (*also known as *Walafrida saxatilis), Lindeneria clavata* and *Helichrysum argyrosphaerum* were often observed in the open savanna habitat type (van Rooyen *et al.* 2001, Le Roux and Schelpe 1988) (Table 3.5).

In the communal and commercial ranches, animals were observed to frequently graze in the open savanna habitat type because the alternative habitat, rocky habitat type is bush encroached. Thus, this habitat type with sandy soil had a high number of poisonous and unpalatable plant species, indicating heavy (or “over”) grazing in this habitat type. *Selago dinteri, Gnidia polycephala*, *B. distich, A. coranica* and *Lindeneria clavata* occurred more abundantly in the open savanna of the communal and commercial ranches than in the game ranch (Table 3.5 and 3.11). *Gnidia polycephala* was also observed by Britz (2004) to be significantly more frequent in communally-managed areas than in other management types. The presence of more unpalatable and poisonous plant species may be a result of the communal management strategy, which usually resulted in high animal densities, leading to overgrazing and land degradation via reduction of palatable plant species while unpalatable and poisonous plants increase (Crawley 1983, Peddie *et al*. 1995).

Palatable plant species (e.g. *Peliostomum leucorrhizum, Monechma incanum, M. divaricatum, Plinthus sericeus*) were frequently detected in rocky habitats, with the exception of the rocky habitat in the communal ranch, which was encroached by unpalatable *Selago dinteri* subsp*. pseudodinteri* and *Geigeria ornativa* (3.10 and 3.11). Although management type had some effects on species composition, habitat type tended to have a greater impact on species composition because a significant difference in Euclidean distances among habitat types was found on both axes (Figure 3.1). From our results, the open savanna and rocky habitat types had an apparent difference in species composition (Figure 3.1). Unpalatable and poisonous plant species were hardly observed in the shrubby habitat type. The shrubby habitat type occurred in an intermediate position on this axis. Thus, the shrubby habitat type may be a transition among pan, rocky and open savanna, resulting in the shrubby habitat type consisting of plant species frequently observed in all other habitat types. This resulted in shrubby habitat type with a higher species diversity index and evenness than other habitat types.

Plant biomass

Mbatha and Ward (in press) observed that plant biomass difference (plant biomass in fenced plots minus plant biomass in unfenced plots) was significantly greater in the commercially-managed area than in the game and communal management types. This difference was attributed to plant material removed by grazing animals and was apparent only after two years of fencing and following a drought. In the present study, plant biomass differed considerably among management types, with the commercial ranch showing the greatest biomass in all seasons. We note that the apparent inconsistency between the result reported on here (higher herbaceous plant biomass in the commercial ranch) and the greater plant biomass difference between fenced and unfenced plots reported on by Mbatha and Ward (in press) may be due to differences in the spatio-temporal nature of grazing effects. That is, higher plant biomass is indicative of lower long-term stocking rate on the commercial ranch while the higher plant biomass difference there is due to the more rapid return of livestock to a particular foraging area.

We further noted that, although the stocking rate in the commercial ranch was lower than in the other ranches (and rotational grazing is practised), plant biomass was low following the drought; this may indicate that land degradation is occurring (Livingstone 1991). The commercial ranch had the highest tree density (in the rocky habitat) of the three ranches and had highest herbaceous plant biomass in the open savanna habitat (communal ranch was lowest), had intermediate densities of unpalatable species, and had lower plant CP and P concentrations in most seasons than other ranches. Again in this study, all these variables show that commercially-managed area has signs of land degradation despite its high plant biomass. Indeed, high plant biomass observed in the commercial ranch may be due to high densities of annuals, unpalatable plants and plants of low nutrient quality.

Among habitat types, open savanna had more plant biomass than other habitat types due to the greater percentage of herbaceous species and grass species forming an understory. Many of these plant species were unpalatable and poisonous (see above). The rocky habitat type did not have high grass and herbaceous plant biomass because it is bush encroached and, consequently, the space for grass and herbaceous species to grow is reduced. The shrubby habitat type is encroached mostly by *T. camphoratus* and *G. flava and* has low grass and herbaceous biomass as a result. Clay soil in the pan habitat type has low infiltration rates that may generate runoff, resulting in slower plant growth rate (Kumar *et al*. 2002) and, eventually, to dwarf plants.

There was a weak negative correlation between plant biomass and plant CP level. This is consistent with Wilson and Minson (1980) and Ruess (1987) who stated that increased biomass often results in reduced CP and other nutrient levels. Eventually, limited soil nutrients are shared by increased aboveground biomass. A weak negative relationship between plant biomass and plant P content was also observed. Clearly, calculations of optimal stocking rate need to take both quality and quantity of plants into account although vegetation quality is probably more important than quantity (see *Estimates of optimal stocking density* below).

Forage quality

In most seasons, the communal management type showed higher CP levels than other management types, in spite of having the lowest soil nitrogen (50% less than the game area). Thus, total soil N content may have little direct effect on plant CP levels. The high density of domestic animal species under communal management may have contributed to enhanced plant CP levels because grazing can change spatial patterns of nutrient accumulation in soil (Dormaar *et al.* 1990, Frank *et al.* 1995, Schuman *et al.* 1999), ultimately resulting in increased accumulation and mineralization of nitrogen in the soil from faeces and urine (Ross and Tate 1984, Augustine and McNaughton 1998, Stark *et al.* 2002). It should be noted that *G. polycephala, L. clavata, S. dinteri* and *G. ornativa* occurred more frequently in the communally-managed area. These plant species often indicate disturbed grazing land and are poisonous and/or unpalatable to livestock (van Rooyen *et al.* 2001). However, it is known that plants with high nutritive value may also be toxic or have low palatability (Hegarty 1982) as a deterrent against herbivory. Thus, high CP content of plant species under communal management type may confer little benefit to herbivores.

Crude protein concentration differed significantly among habitat types only in the dry season of 2003 and wet season of 2004 only, with the pan habitat type showing the highest plant CP levels. Soil chemistry in the pan habitat was observed to be of high quality (see above). Therefore, it is not surprising that plants in the pan habitat type had higher CP levels than in other habitat types, albeit not in all seasons. Habitat-wide, CP content of forage observed in this study during the wet seasons (5.8 – 13.1%) is considered to be of medium to high quality in terms of satisfying animal nutritional requirements. According to Milford and Minson (1965) and Wilson (1982), a CP threshold of 7% is known to limit forage intake. A concentration of CP below the threshold nutritional requirements for growth and reproduction was observed only once in the commercial ranch during the dry season. There was little fluctuation of plant CP content between wet and dry seasons until a drought was broken by heavy rains, which resulted in a rapid increment of 31 to 44% in CP, as also reported by Vallentine (2001) in another study. Indeed, we observed that CP content was positively correlated to annual rainfall, as was found by Orr and Holmes (1984).

Soil P levels differed among management types (when differences among habitat types were controlled). However, this did not result in a difference in plant P content among management types during most of the study period. Plant P content differed significantly among habitats in most periods in this study. Content of plant P in the pan habitat was higher than in other habitat types, probably because it has plant species typical of karooid veld, the only veld type that does not have a P deficiency in South Africa (Schmidt and Snyman 2002). Thus, habitat type, rather than management type, has an important influence on plant quality. When plant P is considered, mean plant P levels observed in our study area were lower than the threshold levels recommended for sheep and cattle (Underwood and Suttle1999, NRC 1996, Holecheck *et al.* 1998). This is not surprising because soils of South Africa are known to be low in P (du Toit *et al.* 1940) and hence the forage plants are also deficient in this mineral. Therefore, supplementation of P is recommended in this area throughout the year in the study area, with the exception of the pan habitat.

The open savanna habitat had high CP and P yields in the most of the wet seasons, while in the dry seasons, the pan habitat had higher CP and P yields than other habitat types. This indicates that pan habitat, unlike open savanna, can sustain animals throughout the year. Indeed, high numbers of wild mammalian herbivores are found in the pan habitat type throughout the year (pers. observation). Grass and herbaceous species are the most abundant species in the open savanna habitat type; their nutrient values fluctuate rapidly between wet and dry seasons as they desiccate and senesce quickly in the dry season (Edwards 1981, Norton 1981). In contrast, plant species in the pan habitat (see above) keep almost constant nutrient values between wet and dry seasons. The shrubby habitat too provides sufficient CP for almost the entire year.

Estimates of optimal stocking density

After high rainfall, plant production and quality increased, resulting in high estimates of optimal stocking density. During the wet seasons, the stocking density estimate based on CP yield was higher than the stocking density estimate based on plant biomass. There was a switch in the dry seasons; optimal stocking density estimates based on CP were less than stocking density based on plant biomass. This may be attributed to low plant biomass and low plant CP concentrations when plants are dead and/or desiccating in the dry seasons. Estimates of stocking biomass based on plant P yield was often less than animal density based on plant biomass and plant CP yield. This is probably due to low soil P levels (except for pan habitat type – see above). A difference of > 50% for optimal stocking density estimates based on plant biomass, plant CP yield and plant P yield between dry and wet seasons was observed in some seasons. These results therefore support the recommendations of Stuth *et al*. (1999) that stocking density recommendations based on plant quality are more conservative and, consequently, more reliable than those based on biomass as the rancher is less likely to exceed the carrying capacity of the land.

Conclusions and recommendations

Ranching a single animal species is not recommended for sustainable use of the grazing land. It has been observed from the present study that the game ranch, with a wide variety of animal species had low bush encroachment, few poisonous and unpalatable plant species and high plant quality. In contrast, the commercial management type, ranching cattle only, showed the lowest dietary quality of parameters measured, had the highest signs of bush encroachment, and many poisonous and unpalatable plant species (but less than in the communal ranch), all indicating land degradation in spite of rotational grazing and lower stocking density than on the communal ranch (see also Mbatha and Ward in press). Our recommendation for the commercially-managed area would be to introduce a greater variety of stock and/or game to reduce selective grazing of certain plant species and its attendant consequences. The communal ranch can also be considered to be degraded, especially close to the inhabited area (see also Smet and Ward 2005).

Our results also indicate that habitats differ considerably in terms of nutrient quality and susceptibility to degradation. In the Northern Cape, where pans are common, these habitats should be judiciously used to optimise stocking densities because of the high nutrient quality throughout the year. Conversely, our study also showed that ranchers should only lightly stock open savanna habitats in spite of high standing biomass because they may be particularly susceptible to degradation and invasion by poisonous and unpalatable plants.

We recommend that a conservative approach to stocking density be adopted by ranchers. Clearly, using the density estimate that is the lowest for any given season can do this but this creates problems for ranchers in terms of selling and buying stock to match these estimates. A more pragmatic strategy may involve using the estimate based on P throughout the year because it is lower than that based on either CP or on plant biomass alone (11 of 15 assessments in each case). This difference is especially pronounced at the end of the dry season when pressure on the sward is most extreme. We recognise that this strategy may result in an excess of forage in the wet season. This can be remedied by leasing land to stockowners with limited rangeland available. We recognize that the abovementioned stocking density estimates are short-term in that they are based on current biomass and nutrient values. They further assume that there will be no long-term degradation caused by these stocking densities. Clearly, it would be most appropriate for ranchers to maintain their own annual estimates of biomass and nutrient quality and to adjust their stocking density estimates accordingly. Using a harvest coefficient of 35% for estimating the stocking rate leaves plant residues that will avoid land degradation, allows sustainable use of rangelands and should provide economic returns even during drought.

References

Acocks JPH 1988. Veld Types of South Africa. Cape Town, Botanical Research Institute.

AOAC 1990. Official Methods of Analysis (15th edn). Association of Official Analytical Chemists. Washington DC, USA.

Archer SR, Schimel DS and Holland EA 1995. Mechanisms of shrubland expansion–land use, climate or CO_2? Climatic Change 29: 91-99.

Augustine DJ and McNaughton SJ 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management 62: 1165–1183.

Barber SA 1984. Soil Nutrient Bioavailability. Wiley, New York.

Barnes DL and McNeil L 1978. Rainfall variability and animal production in the semi-arid savanna of Southern Africa. Proceedings of the Grassland Society of Southern Africa 13: 59-63.

Besag JE and Gleaves JT 1973. On the detection of spatial pattern in plant communities. Bulletin of the International Statistical Institute 45: 153-158.

Bezuidenhout H 1994. An ecological study of the major vegetation communities of the Vaalbos National Park, Northern Cape. 1. The Than-Droogeveld section. Koedoe 37: 19-42.

Bezuidenhout H 1995. An ecological study of the major vegetation communities of the Vaalbos National Park, Northern Cape. 2. The Graspan-Holpan section. Koedoe 38: 65-83

Boyazoglu PA 1973. Mineral imbalances of ruminants in Southern Africa. African Journal of Animal Science 3: 149-152.

Bransby DI 1981. Forage quality. In: Tainton NM (ed) Veld and Pasture Management in South Africa. Shuter and Shooter, Pietemaritzburg. pp 175-191.

Bray RH and Kurtz LT 1945. Determination of total, organic, and available forms of phosphorus in soils. Soil Science 59: 39-45.

Bremner JM 1996. Nitrogen - Total. In: Sparks DL, Page AL, Helmke PA, Loeppert RH, Soltanpour PN, Tabatabai MA, Johnston CT and Sumner ME (eds) Methods of Soil Analysis. Part 3 Chemical Methods. American Society of Agronomy and Soil Science Society of America. Inc. Publisher Madison, USA. pp 1085-1121.

Brinkley D and Vitousek P 1996. Soil Nutrient Availability. In: Pearcy RW, Ehleringer J, Mooney HA and Rundel PW (eds) Plant Physiological Ecology: Field Methods and Instrumentation (5th edn). Chapman and Hall, London. pp 75-96.

Britz M-L 2004. The effects of soil type and management strategy on vegetation structure and function in a semi-arid savanna, South Africa. MSc thesis , University of Stellenbosch, South Africa.

Caughley G and Sinclair ARE 1994. Wildlife Ecology and Management. Blackwell Scientific Publications, Boston.

Christensen NL 1977. Fire and soil-plant nutrient relations in a pine-wiregrass savanna on the coastal plain of North Carolina. Oecologia 31: 27-44.

Crawley MJ 1983. Herbivory: The Dynamics of Animal-Plant Interactions. University of California Press, Los

Angeles.
Cresser M, Killham K and Edwards T 1993. Soil Chemistry and its Applications. Cambridge University Press, Great Britain.
Denton D 1984. The Hunger for Salt. Springer, Berlin.
Donaldson CH and Kelk DM 1970. An investigation of the veld problems of the Molopo area: I. Early findings. Proceedings of the Grassland Society Southern Africa 5: 50-57.
Dormaar JF, Smoliak S and Willms WD 1990. Distribution of nitrogen fractions in grazed and ungrazed fescue grassland Ah horizons. Journal of Range Management 43: 6-9.
Downing BH 1979. Grass protein content and soils as factors affecting area-selective grazing by wild herbivores in the Umfolozi Game Reserve, Zululand. Proceedings of the Grassland Society Southern Africa. 14: 85-88.
Du Toit PF 1972. The goat in the grass-bush community. Proceedings of the Grassland Society of Southern Africa 7: 23-27.
Du Toit PJ, Louw JG and Malan AI 1940. A study of the mineral content and feeding value of natural pastures in the Union if South Africa. Onderstepooort Journal of Veterinary Science and Animal Industry 14: 123-327.
Düvel GH 1995. Resistance against stock reduction: A cognitive field analysis. South African Journal of Ecology 24: 45-60.
Edwards PJ 1981. Grazing management. In: Tainton NM (ed) Veld and Pasture Management in South Africa. Shuter and Shooter, Pietermaritzburg, South Africa. pp 325-334.
Frank AB, Tanaka DL, Hofmann L and Follett RF 1995. Soil carbon and nitrogen of northern Great Plains grasslands as influenced by long-term grazing. Journal of Range Management 48: 470-474.
Freer M 1981. The control of food intake by grazing animals. In: Morely RHW (ed) Grazing Animals. Elsevier, Oxford. pp 105-124.
Greenwood JJD 1996. Basic techniques. In: WJ Sutherland (ed.) Ecological Census Techniques: a Handbook. Cambridge University Press, UK. pp 11-110.
Hardy MB, Barnes DL, Moore A and Kirkman KP 1999. The management of different types of veld. In: Tainton NM (ed) Veld Management in South Africa. University of Natal Press, Pietermaritzburg, South Africa. pp 280-333.
Heitköng IMA and Owen-Smith N 1998. Seasonal selection of soil types and grass swards by roan antelope in a South African savanna. African Journal of Ecology 36: 57-70.
Hatton JC and Smart NOE 1984. The effect of long-term exclusion of large herbivores on soil nutrient status in Murchison Falls National Park, Uganda. African Journal of Ecology 22: 23-30.
Hegarty JB 1982. Deleterious factors in forages affecting animal production. In: Hacker JB (ed) Nutritional Limits to Animal Production from Pastures. Commonwealth Agriculture Bureaux: Farn Royal, UK. pp 133-150.
Hoffman T and Ashwell A 2001. Nature Divided: Land Degradation in South Africa. University of Cape Town Press, South Africa.
Holechek JL, Pieper RD and Herbel CH 1998. Range Management: Principles and Practices (3rd edn). Englewood

Cliffs, Prentice Hall Inc., Upper Saddle River N.J.
Holechek JL, Pieper RD and Herbel CH 2004. Range Management: Principles and Practices (5th edn). Englewood Cliffs, Prentice Hall Inc., Upper Saddle River N.J.
Kiringe JW, Grudkowwska M and Mbatha KR 1999. Predicting diet habitat quality of Nubian ibex (*Capra ibex nubiana*) using faecal analysis. In: Second Mashav International Course on the Conservation of biodiversity in Desert Ecosystems. Jacob Blaustein International Desert Research Center, Ben Gurion Unbiversity of the Negev, Israel. pp 105-121.
Knoepp JD, Coleman DC, Crossley DA and Clark JS 2000. Biological indices of soil quality: an ecosystem case study of their use. Forest Ecology and Management 138: 357-368.
Kovach WL 1999. A MultiVariate Statistical Package for Windows, version 3.1. Kovach Computing Services, Pentraeth, Wales, UK.
Kraaij T. 2002. Effects of rain, nitrogen, fire and grazing on bush encroachment in semi-arid savanna, South Africa. MSc thesis, University of Stellenbosch, South Africa.
Kraaij T and Ward D 2005. Effects of rain, nitrogen, fire and grazing on bush encroachment in semi-arid savanna, South Africa. Plant Ecology in press.
Kumar L, Rietkerk M, van Langevelde F, van de Koppel J, van Andel J, de Ridder N, Stroosnijder L, Skidmore AK and Prins HHT 2002. Relationship between vegetation growth rates at the onset of the wet season and soil type in the Sahelof Burkina Faso: implications for resource utilization at large scales. Ecological Modelling 149: 143-152.
Le Roux A and Schelpe T 1988. Namaqualand: South African Wild Flowers Guide 1. Botanical Society of South Africa, South Africa.
Livingstone I 1991. Livestock management and ‘overgrazing’ among pastoralists. Ambio 20: 80-85.
Low AB and Rebelo ATG 1998. Vegetation of Sout Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria. h
Ludwig JA and Reynolds JE 1988. Statistical Ecology: Primer of Methods and Computing. Wiley and Sons, New York.
Magurran AE 1988. Ecological Diversity and its Measurement. Princeton University Press, New Jersey.
Manly BFJ 1997. Randomization, Bootstrap and Monte Carlo Methods in Biology (2nd edn). Chapman and Hall, London.
Mbatha KR and Ward D 2006. Effects of herbivore exclosures on variation in quality and quantity of plants among management and habitat types in a semi-arid savanna. Journal of Range and Forage Science in press
McCalla GR II, Blackburn WH and Merrill LB 1984. Effects of livestock grazing on sediment production, Edwards Plateau of Texas. Journal of Range Management 37: 211-295.
McDonald P, Edwards RA, Greenhalgh JFD and Morgan CA. 1996. Animal Nutrition (5th edn). Longman, UK.
McDowell LR 1996. Feeding minerals to cattle on pasture. Animal. Feed Science and Technology. 60: 247-271.
McNaughton SJ 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. Ecological Monographs 53: 291-320.

McNaughton SJ 1990. Mineral nutrition and seasonal movements of African migratory ungulates. Nature 334: 343-345.

Milchunas DG, Varnamkhasti AS, Lauenroth WK and Goetz H 1995. Forage quality in relation to long-term grazing history, current-year defoliation, and water resource. Oecologia 101: 366-374.

Milford R and Minson DJ 1965. Determinations of feeding value of pasture and supplementary feeding. Proceedings of the Australian Soociety of Animal Production 6: 319-329.

Morris CD, Hardy MB and Bartholomew PE 1999. Stocking rate. In: Tainton NM (ed) Veld Management in South Africa. University of Natal Press, Pietermaritzburg, South Africa. pp 186-193.

Milliken GA and Johnson DE 1992. Analyses of Messy Data (2nd edn) Vol. 1. Chapman and Hall, New York.

Mueller-Dombois D and Ellenberg H 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons, New York.

Nelson DW and Sommers LE 1982. Total carbon, organic carbon and organic matter. In: Page AL, Miller RH and Keeney DR (eds) Methods of Soil Analysis. Part 2.Chemical and Microbiological Properties. American Society of Agronomy, and Soil Science Society of America, Inc. Publisher. Madison, USA. pp 563-571.

Norton BW 1981. Differences between species in forage quality. In: Hacker JB (ed) Nutritional Limits to Animal Production from Pastures. Commonwealth Agricultural Bureaux. Farnham Royal, UK. pp 89–110.

Noy-Meir I 1995. Interactive effects of fire and grazing on structure and diversity of Mediterranean grasslands. Journal of Vegetatio Science 6: 701-710.

NRC (National Research Council) 1996. Nutrient requirements of Beef Cattle (7th edn). National Academy of Sciences, Washington DC, USA.

Orr DM and Holmes WE 1984. Mitchell Grasslands. In: Harrington GN, Wilson AD and Young MD (eds) Management of Australia's Rangelands. CSIRO, Melbourne, Australia. pp 241-254

Parris R and Child G 1973. The importance of pans to wildlife in the Kalahari and the effects of human settlement on these areas. Journal of South African Wildlife Management Association 3: 1-8.

Peddie GM, Tainton NM and Hardy MB 1995. Effects of past grazing intensity on the vigour of *Themeda triandra* and *Tristachya leucothrix.* African Journal of Forage and Range Science 12: 111-115.

Reid RL and Horvath DJ 1980. Soil chemistry and mineral problems in farm livestock: A review. Animal Feed science and Technology 5: 95-167.

Reynolds WD, Bowman BT, Drury CF, Tan CS and Lu X 2002. Indications of good soil physical quality: density and storage parameters. Geoderma 110: 131-146.

Rhoades JD 1982. Soluble salts. In: Page AL, Miller RH and Keeney DR (eds) Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties. American Society of Agronomy, and Soil Science Society of America, Inc. Publisher. Madison, USA. pp 167-179.

Robbins CT 1993. Wildlife Feeding and Nutrition. Academic Press, London.

Roberts BR 1987. The Availabity of Herbage. In: Hacker JB and Ternouth JH (eds) The nutrition Herbivores. Academic Press, London. pp 47-63.

Ross DJ and Tate KR 1984. Microbial biomass in soil: effects of some experimental variables on biochemical estimations. Soil Biology and Biochemistry 16: 161-167.

Ruess RW 1987. The role of large herbivores in nutrient cycling of tropical savannas. In: Walker BH (ed) Determinants of Tropical Savannas. IRL Press Limited, UK. pp 67-91.

Schmidt AG and Snyman DD 2002. Nutritional and mineral deficiencies, and supplementary feeding. In: Bothma J du P (ed) Game Ranch Management. Van Schalk, Pretoria, South Africa. pp 267-276.

Schuman GE, Reeder JD Manley JT, Hart RH and Manley WA 1999. Impact of grazing managements on the carbon and nitrogen balance of a mixed grass rangeland. Ecological Applications 9: 65-71.

Shapiro SS, Wilk, MB and Chen HJ 1968. A comparative study of various tests of normality. Journal of the American Statistical association 63: 1343-1372.

Skarpe C 1990. Shrub layer dynamics under different herbivore densities in an arid savanna, Botswana. Journal of Applied Ecology 27: 873-885.

Smet M and Ward D 2005. A comparison of the effects of different rangeland management systems on plant species composition, diversity and vegetation structure in a semi-arid savanna. African Journal of Range and Forage Science 22: 59-71.

Smith DA and Schutz EM 1975. Vegetative changes on protected versus grazed desert grassland ranges in Arizona. Journal of Range Management 28: 453-458.

Stark S, Strommer R and Tuomi J 2002. Reindeer grazing and soil microbial processes in two suboceanic and two subcontinental tundra heaths. Oikos 97: 69-78.

StatSoft, Inc. 2002. STATISTICA for Windows [Computer program manual]. Tulsa, OK: StatSoft, Inc, USA.

Stuth JW, Freer M, Dove H and Lyons RK 1999. Nutritional management for free-ranging livestock. In: Jung HG and Fahey GC Jnr (eds) Nutritional Ecology of Herbivores. Proceedings of the Vth International Symposium on the Nutrition of Herbivores, American Society of Animal Science, Savoy, Illinois, USA. pp 696-751.

Tainton NM Veld Management in South Africa 1999. University of Natal Press, Pietermaritzburg, South Africa.

Tainton NM, Aucamp AJ and Danckwerts JE 1999. Grazing programmes. In: Tainton NM (ed) Veld Management in South Africa. University of Natal Press, Pietermaritzburg, South Africa. pp 169-180.

Turner MD 1998. Long-term effects of daily grazing orbits on nutrient availability in Sahelian West Africa: 1. Gradients in the chemical composition of rangeland soils and vegetation. Journal of Biogeography 25: 669-682.

Ulyatt MJ 1973. The feeding value of herbage. In: Butler GW and Bailey RW (eds) Chemistry and Biochemistry of Herbage Vol 3. Edn. Academic Press, London. pp 131-178.

Underwood JE and Suttle NF 1999. The Mineral Nutrition of Livestock (3rd edn). CAB International, New York.

Vallentine JF 2001. Grazing Management. Academic Press, San Diego.

Van Oudtshoorn FP 1994. Guide to Grasses of South Africa. Briza Publications, Cape Town.

Van Riet and Louw Landscape Architects and Metaplan 1999. Kimberley Triangle Community Resource Project. The Kimberley Triangle Forum, Phases one to seven. Pretoria. 53 pp.

Van Rooyen N, Bezuidenhout H and de Kock E 2001. Flowering Plants of the Kalahari Dunes. Ekotrust cc, Lynnwood, South Africa.

Van Soest PJ 1994. Nutritional Ecology of the Ruminants (2nd edn). Comstock Publishing Associates, London.

Walker BH and Knoop WT 1987. The responses of the herbaceous layer in a dystrophic *Burkea africana* savanna to increased levels of nitrogen, phosphate and potassium. Journal of The Grassland Society Southern Africa 4: 31-34.

Ward D, Ngairorue BT, Kathena J, Samuels R and Ofran Y 1998. Land degradation is not a necessary outcome of communal pastoralism in arid Namibia. Journal of Arid Environments 40: 357-371.

Ward D, Saltz D, Rowen M and Schmidt I 1999. Effects of grazing by re-introduced Equus hemionus on the vegetation in a Negev desert erosion cirque. Journal of Vegetation Science 10: 579-586.

Ward D, Saltz D and Ngairorue BT. 2004. Spatio-temporal variation and stock management in arid Namibia. Journal. Range Management. 57: 130-140.

Whitehead DC 2000. Nutrient Elements in Grassland: Soil-Plant-Animal Relationships. Cambridge University Press, Cambridge, United Kingdom.

Wilson JR 1982. Environmental and nutritional factors affecting herbage quality. In: Hacker JB (ed) Nutritional Limits to Animal Production from Pastures. Commonwealth Agriculture Bureaux: Farnham Royal, UK. pp 111-131.

Wilson JR and Minson JD 1980. Prospects for improving the digestibility and intake of tropical grasses. Tropical Grasslands 4: 253-259.

Zacharias PKJ 1986. The use of the cellulase digestion procedure for indexing the dry matter digestibility of forage. Journal of the Grassland Society of Southern Africa 3: 117-121.

Chapter 4

Effects of herbivore exclosures on variation in quality and quantity of plants among management and habitat types in a semi-arid savanna

Abstract

The effects of grazing on plant biomass, plant quality, species evenness, species diversity and species composition were determined among management (communal, commercial and game) types and among habitat (open savanna, rocky and pan) types in a semi-arid savanna. The data were collected over a period of three growing seasons and compared fenced and unfenced plots that were randomly-selected among all management and habitat types. Fenced plots had more plant biomass and greater mean plant height as well as higher CP and P yields, although CP content was higher in unfenced plots. Plant P level was similar between fenced and unfenced plots during the study period. The only significant difference in species composition between fenced and unfenced plots was observed in the pan habitat type during the third growing season, although there was no clear grazing gradient. Negative effects of grazing were more pronounced in the commercially-managed area than under other management types. The open savanna habitat had the highest plant biomass and lowest CP and P levels, while the reverse was true for the pan habitat type. Most parameters assessed showed significant effects between fenced and unfenced plots towards the end of the study only.

Keywords: herbivory, grazing, plant biomass, plant quality, rangeland ecology, rangeland management

Submitted

Mbatha and Ward, Effects of herbivore exclosures on variation in quality and quantity of plants among management and habitat types in a semi-arid savanna to *African Journal of Range and Forage*

Introduction

Inter-annual rainfall variation in savannas has large effects on plant biomass and composition of the sward that, in turn, will affect optimal stocking rates (Varnamkhasti *et al.* 1995, Ward 2004). Semi-arid savannas of southern Africa are subjected to low and erratic rainfall (Barnes and McNeil 1978). Consequently, effects of biotic factors such as grazing on plant community structure and biomass may be masked by this rainfall variation (Ward 2004). Indeed, a number of studies have shown that negative effects of grazing on plant biodiversity do not develop (Behnke and Abel 1996, Ward *et al.* 1998). Thus, it is difficult to discriminate between effects of herbivory and inherent ecosystem variability (*signal* and *noise*) in semi-arid areas (Ward 2004).

Grazing in grassland ecosystems influences plant performance dynamics in a variety of different ways. Grazing has direct effects on plant communities by reducing plant biomass (Hamilton *et al.* 1998). Positive indirect effects of grazing also include improved photosynthetic rates, increased availability of nutrients and reduced water stress for the remaining plants (Wolfson and Tainton 1999). The water stress is reduced because of the reduction of plant transipiring surface by grazing. Grazing animals increase accumulation of nitrogen in the soil due to urea from urine and protein from faeces (Ross and Tate 1984, Stark *et al.* 2002). According to Negi *et al.* (1993) and Turner *et al.* (1993), plants are pre-adapted to repair and compensate to a point when their leaves are removed by grazing mammalian herbivores although these responses depend on plant species, age and part of the plant consumed, environmental conditions and type of grazer. For example, small-mouthed grazers leave little tissue to support regrowth, as opposed to wide mouthed grazers, which are unable to access all plant tissue (Noy-Meir 1993, Van Soest 1994). Thus, grazing by small-mouthed animals can be detrimental to plants because it is vital to retain sufficient green photosynthesizing leaf at all times to maximize regrowth rate (Booysen 1966, Wolfson 1999).

Some studies have shown that plants can compensate for effects of defoliation such that grazed plots had more plant biomass than ungrazed plots (McNaughton 1979, Oesterheld and McNaughton 1988, Turner *et al.* 1993). Increased plant production after grazing may be possible over the short term by inducing plants to photosynthesize and re-mobilize nutrients for regrowth (Turner *et al.* 1993, Rosenthal and Kotanen 1994, Knapp *et al.* 1999). In some studies, plant production was greater in moderately grazed plots than in heavily grazed plots (McNaughton 1979, Turner *et al.* 1993), although Belsky (1986) disputed this. Indeed, when there was heavy grazing for prolonged periods, plant biomass in grazed plots usually declined relative to ungrazed plots (Holechek 2002). This condition is aggravated in semi-arid savanna where drought stress is frequent (Diara 1988, O'Connor 1991). Consequently, range production is decreased especially when coupled with overgrazing (O' Connor 1991). This may result in grasslands being converted to bush-encroached lands (Archer *et al.* 1995, Moleele and Perkins 1998), with a decrease in abundance of perennials and increase in annuals (Andrew 1986, Milchunas and Lauenroth 1993). Thereafter, in natural grazing lands, biodiversity, rare plant species, landscape diversity and perennials will be lost (Milchunas and Noy-Meir 2002). Futhermore, intensive grazing tends to promote the spread of unpalatable plant species through continuous selection of the most palatable grass and herbaceous plants (Gillon 1983). This is crucial because mammalian herbivores depend on natural grassland plant species for their survival (Jones and Wilson 1987).

Pniel Estates, northwest of Kimberley, South Africa, has three management types (game, commercial and communal) on the same soil type. In the game management type, the ranch has a wide range of native antelope (such as *Raphicerus campestris* (steenbok), *Antidorcas marsupialis* (springboks), *Equus burchelli* (zebra), *Hippotragus equinus* (roan), *Connochaetes gnou* and *Connochaetes taurinus* (wildebeest), *Oryx gazella* (gemsbok),*Giraffa camelopardalis* (giraffe),*Tragelaphus strepsiceros* (kudu) and *Ceratotherium simum* (rhinoceros)) to attract hunters and tourists. The stocking density of the game ranch is 10.96 ha LSU^{-1} (Smet and Ward 2005). There are no fenced paddocks within the area and animals are free to graze across the entire game area. A rotational grazing system is practised in the commercial management type. In this management type, beef cattle are ranched for sale on markets and mean stocking rate is 16.ha LSU^{-1} (Smet and Ward 2005). In the communal management type, the rangeland is typically heavily stocked (long-term mean = 9.37 ha LSU^{-1}) (Smet and Ward 2005), supporting diverse livestock (mostly cattle, goats, donkeys, and horses) at levels up to four times the recommended stocking rate based on rainfall and its effects on grass biomass. A continuous grazing system is used in the communally-managed area, with a variable stocking rate (Everson and Hatch 1999). Most livestock is for family consumption and traditional functions (e.g. paying a price for brides, thanksgiving to ancestors) and only seldom will the surplus be sent to market (Tomlinson *et al.* 2002).

The objective of this study was to assess the effects of grazing on plant quality, quantity, species diversity and composition by comparing paired fenced plots (to exclude large mammalian herbivores) and unfenced plots. The effects of management type (game, commercial and communal) and habitat type (rocky, open savanna and pan, shallow depressions that are seasonally inundated) on plant quantity and quality on fenced and unfenced plots were also determined.

Materials and methods

Study site description

The study was conducted on Pniel Estates (25 000ha) situated in the Northern Cape Province, South Africa, located at 28º 36' S, 24º 32' E (1 124m). Pniel Estates consists of a game ranch (10 000ha), a commercial cattle ranch (12 000ha) and a communal ranch (3 000ha). The close proximity of these ranches and the similarity in soil type facilitate comparison of the impacts of game, communal and commercial management on forage quality and quantity in semi-arid savanna.

The vegetation type in this semi-arid savanna, is known as Kimberley Thorn Bushveld (Low and Rebelo 1998) or Kalahari Thornveld (Acocks 1988). In all management types, there is a rocky habitat type, which is characterized by andesite rocks, short grasses, forbs and shrubs (mostly *Acacia mellifera). Acacia mellifera* is encroaching (Kraaij and Ward in press), and seriously reduces grass available to mammalian herbivores and minimizes free movement of ungulates due to its thorniness. The soil type is mainly sandy loam. Open savanna habitat type is also found in all management types. *Acacia erioloba* trees form most of the overstory and the understory consists of a wide diversity of grass species and herbaceous plants in sandy soil. Usually under *A. erioloba,* there are shrubs such as *A. tortilis, Lebeckia linearifolia, Grewia flava, Lycium bosciifolium, L. hirsutum, Tarchonanthus camphoratus* and *Ziziphus mucronata.* The game ranch has two more habitats that do not exist in the commercial and communal management types, namely shrubby and pan habitats. Shrubby habitat is characterized mostly by *T. camphoratus, G. flava*, grass and herbaceous species in sandy clay soil. Pan habitat has vegetation that differs in species and life form composition from the surrounding savanna (Parris and Child 1973) as all plant species are dwarfed. This habitat is seasonally inundated and has dark clay soil. In our study area, the dominant grasses in the clay-pan habitat, *Eragrostis lehmanniana, Cynodon dactylon* and *Eragrostis obtusa*, are all perennials. Apart from these three grass species, *Monechma incanum* and *Asparagus bechuanicus* and *Pentzia* species (especially *P. incana),* a karooid shrub (often associated with the Karoo region of South Africa), are dominant species found on the clay pan habitat.

Climate and soil

The study area forms part of the summer rainfall area in South Africa. The mean annual rainfall for the nearby town, Barkly West, is 388mm and rainfall among years is extremely variable (C.V. = 39%) (Kraaij 2002). Most rain occurs in the form of thunderstorms between January and March, with very little rain between May and October. The temperature varies between -8°C to 41°C, with a mean of 19°C (Low and Rebelo 1998). Daily maximum temperatures exceed 30°C in summer, while for the remainder of the year the days are warm, and the nights in winter are extremely cold (Van Riet and Louw 1999). During the study period from 2001 to 2004, the annual rainfall was 29% above mean rainfall in 2000/2001; was 21% below average in 2001/2002 and in 2002/2003 was 71% below average (severe drought) (Figure 4.1).

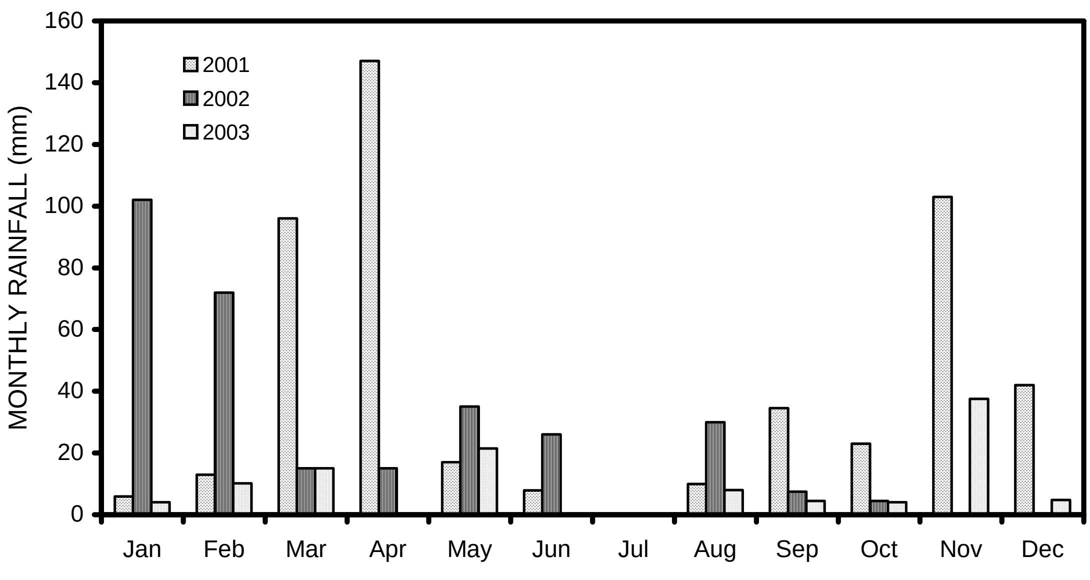

Figure 4.1: Distribution of monthly rainfall at Barkly West during the study period (2001-2003)

Most soils are leached or calcareous due to the hot dry conditions (Low and Rebelo 1998). The soils consist of a thin layer of light brown sandy loam that is underlined by either hard limestone or hard sand loam. The soil type at Pniel varies from moderately deep (0.3 – 0.6m) to deep (> 0.6m) red and yellow sands (Hutton, Clovelly and Kimberley soil forms) to shallow (< 0.3m) and stony (Mispah, Prieska and Glenrosa soil forms) (Bezuidenhout 1995). Sandy soils can be up to 8m deep and consist of 95% quartz (Van Riet and Louw 1999).

Field analyses

In the present study, clipping was used to simulate grazing and compare grazing with non-grazing. Although the clipping technique does not reflect diet selectivity for plant species, plant parts, or account for trampling effects and nutrient recycling by grazing animals (Negi *et al.* 1993), clipping can be considered to simulate non-selective grazing.

Fenced plots were erected at the end of the dry season (September) of 2001 to compare the amount of grass growing inside to that eaten by mammalian herbivores outside fenced plots during the growing seasons. Five permanently fenced plots (5m X 5m) were randomly erected in the rocky and open savanna habitats of game, commercial and communal management types. An unfenced plot (control) with similar vegetation pattern and soil type was demarcated adjacent to all fenced plots to provide 60 experimental plots in all rocky and open savanna habitat types. In addition, ten (3m x 3m) fenced and 10 (3m x 3m) unfenced plots in the pan habitat type of the game management type were added, resulting in total of 80 experimental plots for the study. The fencing was strong and high enough to exclude all large mammalian herbivores found in the study area.

Grass height in fenced and unfenced plots was measured in the growing seasons of 2002, 2003 and 2004 using a Levy bridge technique (Mueller-Dombois and Ellenberg 1974). The Levy bridge point-frequency frame is a quick and effective method of estimating plant height, species composition and percentage cover (Mueller-Dombois and Ellenberg 1974). All plant species observed were recorded in all habitat and management types. Species richness, Shannon diversity index ($\log_2$) (Magurran 1988) and species composition were compared between fenced and unfenced plots as well as habitat and management types of fenced and unfenced plots.

To convert mean plant height values to biomass, we regressed plant height values on biomass assessed from a sub-set of samples in each plot. A 1m x 1m grid was placed over the Levy-bridge in each plot and vegetation within the grid was clipped as close to the ground as possible. This was repeated three times in each plot. Total aboveground plant biomass was calculated by estimating the mean of live and green plant biomass as well as biomass in standing dead plant material within three 1m x 1m grids per plot and mean of three grids was used. The clipped plant samples were dried at 60^0C to constant mass, and milled to pass through a 1mm mesh screen. The difference in plant biomass on fenced and unfenced plots was attributed to removal by grazing mammalian herbivores. Yield of CP and P was calculated for each plot by multiplying percentage concentration and biomass and summing the results.

We used Detrended Correspondence Analysis (DCA) in MVSP (Kovach 1999) to analyze differences in plant species composition among habitat and management types. DCA is an improved multivariate eigenvector technique based on reciprocal averaging, but correcting its main faults (Ward *et al.* 2004). Significance of differences in DCA values between fenced and unfenced plots was tested by comparing Euclidean distances among all pairs of plots on the first two DCA axes. The mean Euclidean distances values of similar plots (i.e. fenced vs. fenced; unfenced vs. unfenced) were compared with mean Euclidean distances between dissimilar plots (fenced vs. unfenced). If the fenced and unfenced plots differ in composition on these two axes then mean Euclidean distances between similar plots should be smaller than between dissimilar plots. Conversely, if fenced and unfenced plots do not differ in species composition, there should be no significant difference between mean Euclidean distances for similar and dissimilar plots. Bootstrapping was used to compare Euclidean distances (Manly 1997) because they do not conform to a normal distribution (see e.g. Ward *et al.* 1999); specifically, we compared the actual mean difference between similar and dissimilar plots with mean differences from 1000 random re-arrangements of DCA values among plots. If the actual difference is greater than the random difference at least 950 times out of 1000, the difference between fenced and unfenced plots is statistically significant at $\alpha = 0.05$. We note that this procedure is analogous to the ANOSIM procedure performed in the PRIMER statistical package (Ludwig and Reynolds 1988).

Laboratory analyses

Crude protein (CP) of plant concentrations was determined using a standard Kjeldahl technique (AOAC 1990). Phosphorus (P) concentrations were ascertained spectrophotometrically according to the micro technique of the AOAC (1990). The high fibre content of certain grass species reduces the nutritional value to animals in spite of relatively high energy and protein contents. Hence, the dry matter digestibility of grass species was indexed by the *in vitro* digestible dry matter method of Zacharias (1986) because this technique incorporates concentrations, ratios and structures of forage constituents in an index of potential for breakdown by rumen microbial populations (Milchunas *et al.* 1995).

Statistical analyses

Normality of data distribution was confirmed by the Shapiro-Wilks' test (Shapiro *et al.* 1968, StatSoft 2002). Differences among fenced and unfenced plots of various management and habitat type were measured by randomized block ANOVA. Type III sums of squares were used for ANOVA (Milliken and Johnson 1992). Where necessary, data were transformed to meet the requirements of parametric analyses. Scheffe *post hoc* comparisons of means were performed on plant biomass, height, CP, P and all soil chemical characteristics in fenced and unfenced plots of different management and habitat types. Pearson product-moment correlation analyses were used for comparisons of plant height and plant biomass, plant biomass and plant CP, plant biomass and P and among soil characteristics.

Results

Plant height in fenced and unfenced plots

There was no significant difference ($F_{1, 698} = 2.04$, $P = 0.15$) in plant height between fenced and unfenced plots in 2002. In contrast, plant height differed significantly ($F_{1, 672} = 5.89$, $P = 0.02$ and $F_{1, 697} = 109.48$, $P < 0.001$) between fencing types in 2003 and 2004, respectively (Table 4.1).

Table 4.1: Effects of fencing on plant height (cm ± SE) and plant biomass (g/m^2) on Pniel Estates in the 2003 and 2004 growing seasons

Year	Fencing	Height (cm)	Biomass (g/m^2)
2003	Unfenced	8.62 ± 0.63	30.35 ± 2.56
	Fenced	10.79 ± 0.63	43.17 ± 2.56
2004	Unfenced	8.04 ± 0.28	40.73 ± 3.24
	Fenced	12.23 ± 0.28	62.94 ± 3.24

Management type had a non-significant influence ($F_{2, 697} = 1.84$, $P = 0.16$) in plant height in the growing season of 2002. A significant difference ($F_{2, 671} = 5.24$, $P = 0.006$ and $F_{2, 696} = 19.76$, $P < 0.001$) in the effects of management types in plant height was shown in 2003 and 2004, respectively (Table 4.2). Scheffe *post hoc* tests showed that, in 2003, unfenced plants in the commercial management type were taller than plants in the communal management type and in 2004 plant height was the greatest in the commercial management type in fenced plots. There was a significant difference $F_{2, 697} = 39.04$; $P < 0.001$ in plant height among habitat types in 2002. Similarly, a significant difference ($F_{2, 671} = 13.38$, $P < 0.001$ and $F_{2, 696} = 89.26$, $P < 0.001$) in plant height among habitat types was observed in 2003 and 2004, respectively (Table 4.3). Plants in the pan habitat type were the shortest during the study (Scheffe *post hoc* test, $p < 0.05$).

Table 4.2: Effects of management type on plant height (cm ± SE) and plant biomass (g/m^2) of fenced and unfenced plots on Pniel Estates in the 2003 and 2004 growing seasons

Year	Management	Fenced Height (cm)	Fenced Biomass (g/m^2)	Unfenced Height (cm)	Unfenced Biomass (g/m^2)
2003	Game	9.91 ± 0.67	37.09 ± 2.87	5.39 ± 0.34	36.64 ± 2.25
	Communal	7.53 ± 0.86	31.65 ± 3.83	4.31 ± 0.26	27.34 ± 2.30
	Commercial	11.35 ± 0.81	40.82 ± 3.63	9.12 ± 0.45	36.98 ± 2.37
2004	Game	9.67 ± 0.32	49.65 ± 3.95	4.73 ± 0.26	42.15 ± 3.26
	Communal	8.82 ± 0.39	49.60 ± 4.99	3.89 ± 0.28	40.49 ± 2.49
	Commercial	12.15 ± 0.39	57.57 ± 4.99	4.92 ± 0.32	38.71 ± 3.35

Plant biomass in unfenced and fenced plots

Management, fencing and habitat types did not have significant effects (range in P = 0. 07 – 0.23) on plant biomass in the growing season of 2002. In 2003 and 2004, plant biomass differed significantly ($F_{1, 68} = 12.52$, $P < 0.001$ and $F_{1, 70} = 23.51$, $P < 0.001$ respectively) between fenced and unfenced plots (Table 4.1).

Table 4.3: Mean values of plant height (cm ± SE) and plant biomass (g/m^2 ± SE) among habitat types in the fenced and unfenced plots during the growing seasons of 2003-2004 on Pniel Estates

Year	Habitat	Fenced Height (cm)	Fenced Biomass (g/m^2)	Unfenced Height (cm)	Unfenced Biomass (g/m^2)
2003	Open savanna	12.19 ± 0.68	46.27 ± 2.96	11.52 ± 2.13	39.92 ± 2.27
	Rocky	10.63 ± 0.66	38.88 ± 2.86	7.12 ± 0.37	27.88 ± 3.20
	Pans	6.87 ± 1.59	36.24 ± 4.52	5.17 ± 0.58	25.49 ± 2.76
2004	Open savanna	14.86 ± 0.39	64.19 ± 3.60	11.23 ± 0.46	49.63 ± 3.26
	Rocky	10.75 ± 0.37	48.62. ± 5.69	5.96 ± 0.34	32.44 ± 3.25
	Pans	8.79 ± 0.55	58.71 ± 5.69	4.73 ± 0.44	39.23 ± 4.78

Plant biomass did not differ significantly among management types in 2003 and 2004 ($F_{2, 67} = 1.50$, P = 0.2 and $F_{2, 69} = 0.91$, P = 0.41, respectively-Table 4.2). In contrast, habitat types had a significant effect ($F_{2, 67} = 4.09$, P = 0.02 and $F_{2, 69} = 10.86$, P < 0.001) on plant biomass in 2003 and 2004, respectively (Table 4.3). From Scheffe *post hoc* tests, the open savanna habitat had greater plant biomass than the pan habitat type in 2003 and more than the rocky habitat type in 2004.

The difference (plant biomass in fenced plots minus plant biomass in unfenced plots) of plant biomass between fenced and unfenced plots was not significantly different from zero (range in P = 0.06 – 0.29). Similarly, habitat types did not show a significant effect ($F_{2,33} = 0.22$, P = 0.80 and $F_{2, 33}$ = 1,29, P = 0.29) in plant biomass difference between fenced and unfenced plots. The difference in plant biomass of fenced and unfenced plots varied significantly among management types in the growing seasons of 2003 and 2004 ($F_{2, 33} = 3.68$, P = 0.04 and $F_{2, 33} = 3.96$, P = 0.03, respectively). From Scheffe *post hoc* tests, the commercially-managed area displayed the biggest difference between fenced and unfenced plots.

Plant species richness, diversity and composition in fenced and unfenced plots

There was no significant effect (ranged between P = 0.5 - 0.9) of fencing on plant diversity and species richness during the study period. Species composition did not differ (P > 0.05) between fenced and unfenced plots during most of the study period, although in the growing season of 2004 only, species composition of pan habitat differed significantly between fenced and unfenced plots (P = 0.005, Figure 4.1). Detrended Correspondence Analysis of plant composition for pan habitat data showed that 19.5% of variance was explained by the first axis and 12.95% of variance was explained by the second axis. The differences between the fenced and unfenced plots were generally small, and few showed large differences between fenced and unfenced plots. The differences between fenced and unfenced plots of pan habitat were not all in the same direction, indicating that there is no consistent grazing gradient on the multivariate axes (Figure 4.1). *E. lehmanniana* was more frequently observed in fenced plots than unfenced plots of the pan habitat, showing high sensitivity to grazing.

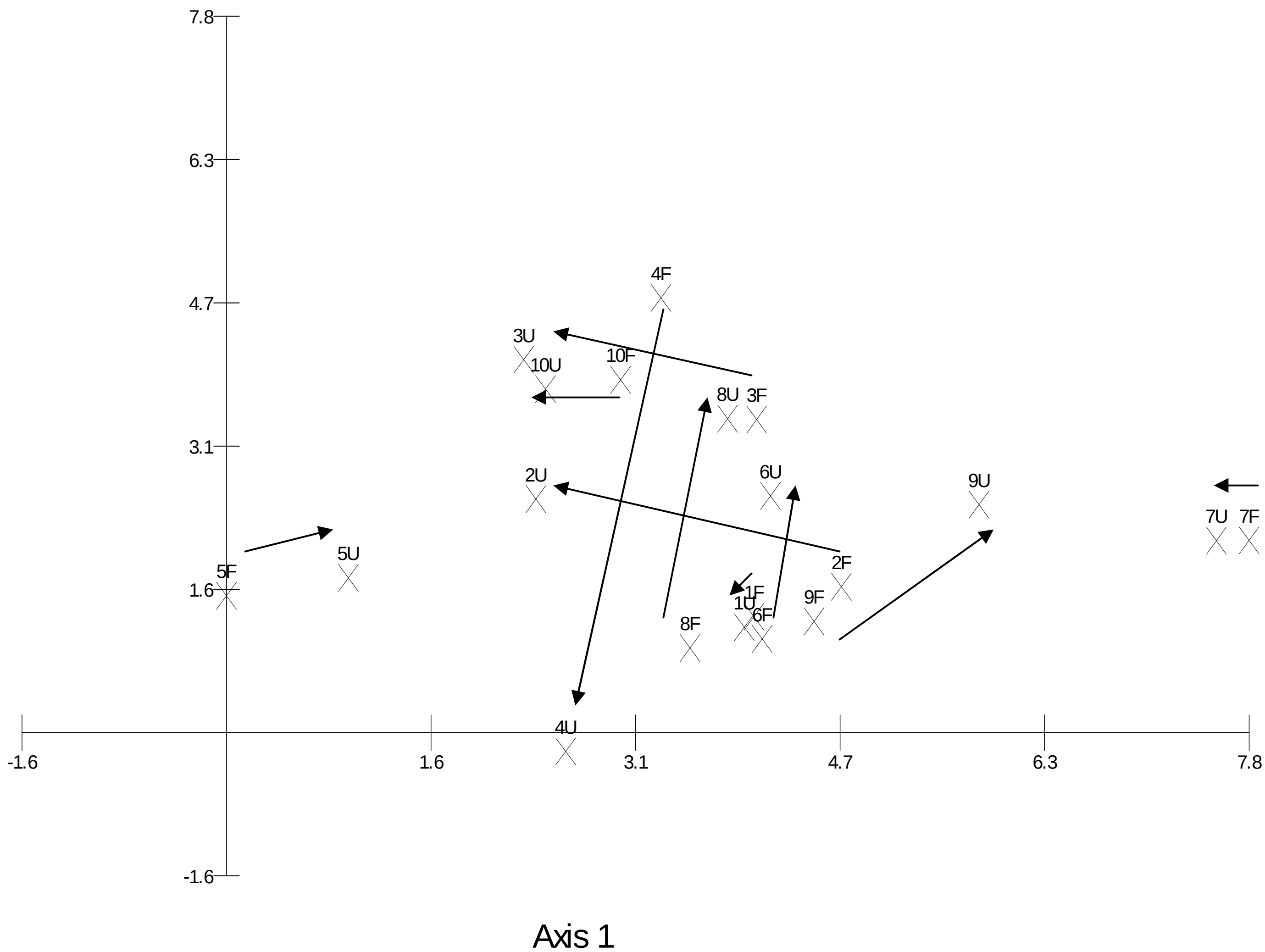

Figure 4.2: First and second axes of a Detrended Correspondence Analysis of plant composition for pan habitat type in the 2004 growing season. 19.5% of variance is explained by the first axis and 12.95% is explained by the second axis. Numbers indicate plot numbers. F = fenced plot and U = unfenced plot. Note that there is no consistent pattern in differences among paired fenced and unfenced plots (see directions of change indicated by arrows) indicating that there is no grazing gradient.

A significant difference ($F_{2, 77} = 3.62$, $P = 0.03$ and $F_{2, 77} = 3.57$, $P = 0.03$) in 2003 and 2004 growing seasons was observed among management types of fenced and unfenced plots in terms of species diversity. From *post hoc* tests, the communally-managed area had greater species diversity than other management types. In 2004 only, habitat types of fenced and unfenced plots had a significant influence ($F_{2, 77} = 18.37$, $P < 0.001$) on plant species diversity. The pan habitat type had lower plant diversity than open savanna and rocky habitat types (Scheffe *post hoc* test, $p < 0.05$). Species richness did not show significant differences among management and habitat types during the study period.

Plant quality in fenced and unfenced plots

Plant CP concentration differed non-significantly ($F_{1, 67} = 0.09$, $P = 0.76$) between fenced and unfenced plots in the growing season of 2003. Fencing had a significant effect ($F_{1, 70} = 6.62$, $P = 0.01$) in plant CP concentration in the growing season of 2004 (Table 4.4).

Table 4.4: Effects of fencing on plant CP and P concentrations (% ± SE) on Pniel Estates in the 2003 and 2004 growing seasons

Year	Fencing	CP (%)	P (%)
2003	Unfenced	8.69 ± 0.25	0.10 ± 0.005
	Fenced	8.79 ± 0.26	0.11 ± 0.005
2004	Unfenced	10.10 ± 0.33	0.10 ± 0.006
	Fenced	9.50 ± 0.33	0.10 ± 0.006

In the growing season of 2003, plant CP concentration varied non-significantly ($F_{2, 66} = 3.13$, $P = 0.51$) among habitat types between fenced and unfenced plots (Table 4.6). Similarly, management types had no significant effect ($F_{2, 66} = 0.78$, $P = 0.46$) on plant CP concentration (Table 4.5). In 2004, management and habitat types had significant effects ($F_{2, 69} = 5.96$, $P = 0.004$ and $_{F2, 69} = 9.154$, $P < 0.001$; Table 4.5 and 4.6, respectively) on plant CP concentration. In Scheffe *post hoc* tests, the pan habitat type had a significantly higher CP concentration than open savanna and rocky habitat types. The commercial management type had significantly lower CP concentrations than game and communal management types.

There was a non-significant effect ($F_{1, 67} = 0.09$, $P = 0.76$) of fencing on plant CP yield (= percentage of CP concentration x biomass) in 2003. Fencing had a significant influence ($F_{1, 70} = 6.62$, $P = 0.01$) on plant CP yield in 2004. Crude protein yield differed non-significantly among management types in the growing seasons of 2003 and 2004 ($F_{2, 66} = 1.09$ $P = 0.34$ and $F_{2, 69} = 0.01$, $P = 0.91$, respectively). In the growing seasons of 2003 and 2004, a significant influence ($F_{2, 66} = 3.82$ $P = 0.03$ and $F_{2, 69} = 13.71$, $P < 0.001$, respectively) of CP yield was observed among habitat types. The rocky habitat showed the lowest CP yield and open savanna habitat had the highest during the study period (Scheffe *post hoc* test, $p < 0.05$). Similarly, a significant influence ($F_{1, 67} = 12.11$, $P < 0.001$ and $F_{1, 70} = 10.15$, $P = 0.002$) of fencing was shown on CP yield in the growing seasons of 2002 and 2004, respectively. Plant CP production yield differed significantly ($F_{2, 66} = 3.82$ $P = 0.03$ and $_{F\ 2, 69} = 13.71$, $P < 0.001$) in 2003 and 2004, respectively, among habitat types.

Table 4.5: Effects of management types on plant CP and P content (% ± SE) on Pniel Estates in the 2003 and 2004 growing seasons

Year	Management	CP (%)	P (%)
2003	Game	8.78 ± 0.26	0.12 ± 0.004
	Communal	9.02 ± 0.35	0.11 ± 0.006
	Commercial	8.42 ± 0.34	0.09 ± 0.006
2004	Game	10.68 ± 0.34	0.12 ± 0.006
	Communal	10.42 ± 0.43	0.10 ± 0.008
	Commercial	8.86 ± 0.43	0.08 ± 0.008

A non-significant difference between fenced and unfenced plots was observed in plant P concentration in the 2003 and 2004 growing seasons ($F_{1, 67} = 0.23$, $P = 0.63$ and $F_{1, 70} = 0.28$, $P = 0.6$) respectively (Table 4.4). Plant P level differed significantly among management types ($F_{2, 66} = 9.51$, $P < 0.001$ and $F_{2, 69} = 5.93$, $P = 0.004$) in the growing seasons of 2003 and 2004, respectively (Table 4.5). The game management type had significantly higher plant P than in the commercially managed area in both seasons according to *post hoc* tests. Similarly, habitat types had a significant influence in plant P in the wet seasons of 2003 and 2004 ($F_{2, 66} = 28.61$, $P < 0.001$ and $F_{2, 69} = 39.95$, $P < 0.001$, respectively Table 4.6). From *post hoc* tests, in both growing seasons, pans had a significantly higher plant P level than open savanna and rocky habitat types.

Table 4.6: Effects of habitat types on plant CP and P levels (% ± SE) on Pniel Estates in the 2003 and 2004 growing seasons

Year	Habitat	CP (%)	P (%)
2003	Open savanna	8.75 ± 0.27	0.09 ± 0.004
	Rocky	8.38 ± 0.27	0.10 ± 0.004
	Grassy pans	9.61 ± 0.41	0.15 ± 0.006
2004	Open savanna	9.97 ± 0.34	0.09 ± 0.005
	Rocky	9.43 ± 0.34	0.09 ± 0.005
	Grassy pans	12.11 ± 0.53	0.16 ± 0.007

Phosphorus mass yield did not differ significantly among management types ($F_{2, 66} = 1.41$, $P = 0.25$ and $F_{2, 69} = 1.08$, $P = 0.34$) in 2003 and 2004, respectively. There was a significant difference ($F_{2, 66} = 2.99$, P 0.047 and $F_{2, 69} = 13.09$, $P < 0.001$) in P yield among habitats in 2003 and 2004, respectively. From *post hoc* tests, pan habitat had a significantly higher P yield in 2003 than the open savanna and rocky habitat types. Similarly, in 2003 and 2004, a significant influence ($F_{1, 67} = 9.01$, $P = 0.004$ and $F_{1, 70} = 8.40$, $P = 0.005$, respectively) of fencing was observed on P yield, with fenced plots showing higher P mass than in unfenced plots. Plant P yield was not significantly different ($F_{2, 66} = 2.69$, $P = 0.07$) in 2003, but differed significantly ($F_{2, 69} = 13.09$, $P < 0.001$) in 2004 among habitat types.

Discussion

Effects of fencing

In the 2002 growing season, fencing had no influence on all diet parameters measured. This can be attributed to the short period after fences were erected. Grazing had negative effects on plant height and biomass, resulting in more plant biomass and greater height in fenced plots than unfenced plots as from the second year of the study. This is accredited to grazing mammalian herbivores that persistently remove leaf tissue in unfenced plots. However, grazing of the previous year's growth may allow herbivores to eat plants of high quality by producing green tissue that is unobstructed by dead and standing plant tissue (Knapp and Seastedt 1982, McNaughton 1984, McNaughton 1992). Furthermore, a higher level of CP in regrowth leaves than in the newly initiated leaves of ungrazed plants has been recorded (Jameson 1963). The result under these scenarios was the higher concentration of CP in unfenced plots than fenced plots that was apparent in the third year of this study. Thus, unfenced plots in semi-arid savanna had lower biomass but more CP content, as also observed by Penning de Vries and Djitèye (1982, in Bergström and Skarpe 1999) in dry savanna. The improved content of plant CP may also be due to increased availability of soil nitrogen and other resources per plant, owing to a decline in plant biomass and high young: old plant tissue after grazing. It is also possible that the increased accumulation of nitrogen (% CP = 6.25 x nitrogen concentration) from urine and faecal deposition (Ross and Tate 1984, Day and Detling 1990, Whitehead 2000) increased nutritional quality of plants for mammalian herbivores. Consequently, there was more plant CP content despite lower plant biomass. The delayed CP concentration difference (observed for the first time in 2004) may be accredited to the short time after fence construction (2 years) and annual rainfall that was 71% below the mean annual rainfall in 2002/2003. The timing and drought also resulted in similar P content between fenced and unfenced plots during our study period. The drought affected plant P content because P level is usually positively correlated with the amount of soil moisture (Reid and Horvath 1980, Norton 1981). We also observed that the concentration of plant CP was less when rainfall was low and more when rainfall was high, indicating a positive correlation between rainfall amount and CP concentration in semi-arid savanna ecosystems.

In the present study, fenced plots had significantly higher CP and P yield (concentration x biomass) than unfenced plots. These results are consistent with observations by Ritchie *et al.* (1998) and Wilms *et al.* (2002) after more than five years of excluding herbivores. In contrast, Turner *et al.* (1993) observed higher CP and P yield on mowed plots than on plots not mowed for ten years. Milchunas *et al.* (1995) noticed that nitrogen yields in grazed plots were greater in long-term grazed plots than in ungrazed plots in a simulated wet year after 21 years of data collection. It appears that when time after construction of fenced plots is long, CP and P yields in unfenced plots exceed CP and P yield in fenced plots because grazing animals can alter amounts and composition of nutrient accumulation in the soil, eventually affecting soil nitrogen dynamics, plant species composition and ecosystem structure of grasslands (Fuhlendorf *et al.* 2002). Thus, fenced plots in this study had higher CP and P yields because the short period (2 years) after erecting fences, and accumulation of urine and faeces deposition in the unfenced plots, is not yet sufficient to result in higher CP and P yields. We predict that if data are collected again later there will be a switch in nutrient yield in fenced and unfenced plots. Plant biomass was strongly and positively correlated with plant CP and P yield (r = 0.9 and r = 0.7, respectively) across seasons. These results are consistent with the observation by Wilms *et al.* (2002).

Plant species evenness and diversity between fenced and unfenced plots were similar for the study period. These results are consistent with the observation of Belsky (1986) and Ward *et al.* (1999) who noticed that species composition in fenced and unfenced plots were similar initially but became more different after five years of study as species composition in fenced plots was altered by competition between species normally suppressed by grazing. A significant difference in plant composition was observed in 2004 only between fenced and unfenced plots in the pan habitat, where changes were inconsistent in form (see directions of arrows in Figure 4.1). This change in species composition in the pan habitat can be accredited to short herbaceous and grass species there that are sensitive to heavy grazing (Belsky 1992). Protection from grazing led plants to grow to their maximum heights. These differences between fenced and unfenced plots varied a lot: some were very small (e.g. plot 1 and 7), although there were pairs of plots showing large differences (e.g. plot 2 and plot 4) (Figure 4.1). This shows that the effects of grazing on plant composition are not yet pronounced enough to create a grazing gradient in multivariate space and that there are many factors currently affecting species composition. These results indicate that the effects of grazing on plant composition of fenced and unfenced plots do not exist immediately after erecting fences, but habitats such as pan habitat may show the effects sooner than others. Only *E. lehmanniana* was observed to invade many fenced plots, indicating that this grass species is sensitive to grazing (see also Smet and Ward 2005). Species such as *Cynodon dactylon* and *Felicia filifolia* that are known to be palatable.also seem to be sensitive to grazing because they were observed only in fenced plots, although they were not common in many plots.

Effects of management types on fenced and unfenced plots

We controlled for spatial variation between fenced and unfenced plots in each management type. Plant height differed among management types in the growing seasons of 2003 and 2004, with plants in the commercially-managed area being taller than in other management types, as also observed by Smet and Ward (2005). It is interesting that this significant difference in plant height did not result in a significant difference in plant biomass among fenced and unfenced plots of different management types during the study. This can be attributed to low leaf production of tall grass species such as *Pogonarthria squarrosa, Schmidtia pappophoroides* and *Eragrostis lehmanniana* frequently observed in the fenced plots of all management types. These grass species are tall but their contribution to biomass is low (Russell *et al.* 1991, van Oudtshoorn 1999).

Surprisingly, the difference (fenced plant biomass minus unfenced plant biomass) in plant biomass between fenced and unfenced plots among management types was observed in the commercial ranch only. This difference was strong and took two years to become apparent and was attributed to plant material removed by grazing mammalian herbivores. This may indicate that the negative effects of grazing in the commercially-managed area are greater than in other management types. In contrast, Smet and Ward (2005) did not observe negative effects in the commercially-managed area. This contradiction may be related to the fact that Smet and Ward (2005) focused on piospheres and placed transects around water-points only (with predominantly clay soils), while in the present study, plots were randomly-selected in different habitat types with diverse soil types. In the commercial management type, the rotational grazing system has been practised since the early 1960's. The greater negative effects of grazing in this ranch than the other ranches may be due to the presence of a single animal species (cattle). This is not surprising because a single animal species may result in selective grazing that causes long-term degradation (Illius and O'Connor 1999). A possible negative effect of using a rotational grazing system may be that animals are re-introduced to a paddock before the plants have fully recovered from the previous bout of heavy grazing. It is also possible that the low and erratic rainfall characterizing our study area exacerbated the delay in the recovery of grazed plants (cf. Ward *et al*. 2004). The reason that other management types did not show this difference might be due to the greater diversity of animal species (monogastric and ruminants: grazers, mixed-feeders and browsers (kudu and giraffe in game area)), and that animals are not restricted by fences and may change habitat type in different seasons, thereby lowering stocking density in sensitive habitats. The game area has the most different feeder types (grazers, mixed-feeders and browsers) and animals range freely and, thus, showed the least negative effects of grazing.

Plant CP level differences among management types became apparent for the first time after two years of fencing. After a year, plant P content differences became apparent, with the commercial ranch showing the lowest plant P content. From the above, it can be seen that the commercial management type had the lowest CP and P content and the game management type had the highest P levels despite the low plant biomass. Thus, high plant quantity does not guarantee high plant quality.

Among management types, a significant difference in terms of species diversity was observed. The communal ranch was more diverse in terms of plant species than the commercial and game management types. This diversity is attributed to a greater number of poisonous plant species in the communal ranch (Mbatha and Ward in prep). The results of this study also revealed that, in terms of plant species diversity and evenness, significant habitat type effects on fenced and unfenced plots occurred from the second year only (2004).

Effects of habitat types on fenced and unfenced plots

Spatial variation between fenced and unfenced plots in each habitat type was also controlled for. Open savanna plants were taller and had greater biomass than other habitat types; this can be accredited to the presence of more tall grass species (*Pogonarthria squarrosa, Schmidtia pappophoroides* and *Eragrostis lehmanniana*) in this habitat type. Pans had the lowest plant biomass and plant height throughout the study. This is not surprising because the pan habitat type is characterized by short grass and dwarf plant species (Bergstrom and Skarpe 1999, Mbatha and Ward in prep). The rocky habitat type had intermediate plant height and biomass. This can be attributed to bush encroachment by *A. mellifera* in this habitat type (Kraaij 2002). Bush encroachment has a tendency of reducing the area available for grass and herbaceous plants to grow (Archer *et al.* 1995).

Differences in plant CP and P levels took only one year to be apparent among habitat types, with pan habitat showing higher concentrations than other habitat types due to high soil quality and the presence of karooid plant species known to be high in nutrients (Boyazoglu 1973, Le Roux and Schelpe 1988). The pan habitat type had lower plant diversity and evenness than the rocky and open savanna habitat types. Lower grass species diversity in the pan habitat type than in the rocky and open savanna habitat types contributed to lower plant species diversity in the pan habitat. Moreover, herbaceous plants were less common in the pans than in open savanna and rocky habitat types.

Conclusion and management implications

The negative effects of grazing were more evident in the commercial ranch. In a rotational grazing system, these effects are probably due to returning herds to camps before the plants have had time to recover and, perhaps, due to the use of a single species of livestock, which increases the negative impacts of selective grazing. This problem may be more acute in areas such as this with low and erratic rainfall, which makes it difficult for ranchers to consistently follow a regular rotation of animals among camps. Clearly, ranchers need to follow a more flexible system of rotation and need to examine the state of the sward, moving animals into new camps only once they have recovered sufficiently from the previous period of grazing.

It is evident from our study that exclosures are very useful tools for examining the effects of grazing on plant quality and composition. However, in areas such as this, where inter-annual rainfall variation is high, negative effects of grazing are likely to be detected after a number of years (in our case, three years – see also Ward *et al.* 1998, 2004). Consequently, we recommend that ranchers use exclosures as medium- to long-term indicators of range condition in semi-arid savannas.

References

Acocks JPH 1988. Veld types of South Africa. Cape Town, Botanical Research Institute.

Andrew MH 1986. Use of fire for spelling monsoon tallgrass pasture grazed by cattle. Tropical Grassland 20: 66-77.

AOAC 1990. Official Methods of Analysis (15th edn). Association of Official Analytical Chemists, Washington DC, USA.

Archer SR, Schimel DS and Holland EA 1995. Mechanisms of shrubland expansion–land use, climate or CO_2? Climatic Change 29: 91-99.

Barnes DL and McNeil L 1978. Rainfall variability and animal production in the semi-arid savanna of southern Africa. Proceedings of the Grassland Society of Southern Africa 13: 59-63.

Behnke R and Abel N 1996. Revisited: the overstocking controversy in semi-arid Africa. World Animal Review 87: 4-27.

Belsky AJ 1986. Revegetation of artificial disturbances in grasslands of the Serengeti National Park, Tanzania II. Five years of successional change. Journal of Ecology 74: 937-952.

Belsky AJ 1992. Effects of grazing, composition, disturbance and fire on species competition and diversity in grassland communities. Journal of Vegetation Science 3: 187-200.

Bergström R and Skarpe C 1999. The abundance of large wild herbivores in semi-arid savanna in relation to seasons, pans and livestock. African Journal of Ecology 37: 12-26.

Bezuidenhout H 1995. An ecological study of the major vegetation communities of the Vaalbos National Park, Northern Cape. 2. The Graspan-Holpan section. Koedoe 38: 65-83

Booysen P deV 1966. A physiological approach to research in pasture utilization. Proceedings of the Grassland Society of Southern Africa 1: 77-96.

Boyazoglu PA 1973. Mineral imbalances of ruminants in southern Africa. African Journal of Animal Science 3: 49-152.

Day TA and Detling JK 1990. Grassland patch dynamics and herbivore grazing preference following urine deposition. Ecology 63: 180-188.

Diara L 1988. Changes in *Vetiveria nigritiana* and *Eragrostis barteri* grasslands in the Niger flood plain, central Mali. ILCA Bulletin 31: 14-18

Everson TM and Hatch GP 1999. Managing veld (rangeland) in the communal areas of southern Africa. In: Tainton NM (ed) Veld Management in South Africa. University of Natal Press, Pietermaritzburg, South Africa. pp 381-388.

Fuhlendorf SD, Zhang H, Tunnel TR, Engle DM and Cross AE 2002. Effects of grazing on restoration of southern mixed prairie soils. Restoration Ecology 10: 401-407.

Gillon D 1983. The fire problem in tropical savannas. In: Bourliere F (ed) Ecosystems of the World Vol. 13: Tropical Savannas. Elservier Science, Amsterdam. pp 617-641.

Hamilton WE, Giovannini MS, Moses SA, Coleman JS, McNaughton SJ 1998. Biomass and mineral element responses of a Serengeti short-grass species to nitrogen supply and defoliation: compensation requires a critical [N]. Oecologia 116: 407–418.

Holecheck JL 2002. Do most livestock losses to poisonous plants result in “poor” range management? Journal of Range and Management 55: 270-276.

Illius AW and O’Connor TG 1999. On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. Ecological Applications 9: 789-813.

Jameson DA 1963 Responses of individual plants to harvesting. Botanical Review 29: 532-594.

Jones DIH and Wilson AD 1987. Nutritive quality of forage. In: Hacker JB and Ternouth JH (eds) The nutrition of herbivores. Academia Press, Australia. pp 65- 89.

Kovach WL 1999. A MultiVariate Statistical Package for Windows, version 3.1. Kovach Computing Services, Pentraeth, Wales, UK.

Knapp AK and Seastedt TR 1986. Detritus accumulation limits productivity of a tallgrass prairie. Bioscience 36: 662-668.

Knapp AK, Blair JM, Briggs JM, Collins SL, Hartnett DC, Johnson LC, and Towne EG 1999. Keystone role of bison in North American tallgrass prairie. Bioscience 49: 39-5.

Kraaij T 2002. Effects of rain, nitrogen, fire and grazing on bush encroachment in semi-arid savanna, South Africa. MSc thesis, University of Stellenbosch, Stellenbosch, South Africa.

Kraaij T and Ward D 2005. Effects of rain, nitrogen, fire and grazing on bush encroachment in semi-arid savanna, South Africa. Plant Ecology in press

Le Roux A and Schelpe T 1988. Namaqualand: South African wild flower guide 1. Botanical Society of South Africa, South Africa.

Low AB and Rebelo ATG 1998. Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria.

Ludwig JA and Reynolds JE 1988. Statistical ecology: Primer of methods and computing. Wiley and Sons, New York.

Magurran AE 1988. Ecological Diversity and its Measurement. Princeton University Press, New Jersey.

Manly BFJ 1997. Randomization, Bootstrap and Monte Carlo Methods in Biology. 2nd ed. Chapman and Hall, London.

McNaughton SJ 1979. Grazing as an optimization process: Grass-ungulate relationships in the Serengeti. American Naturalist 113: 691-703.

McNaughton SJ 1984. Ecology of a grazing ecosystem: The Serengeti. Ecological Monographs 55: 259-294.

McNaughton SJ 1992. Laboratory-simulated grazing: interactive effects of defoliation and canopy closure on Serengeti grasses. Ecology 73: 170-182.

Milchunas DG and Lauenroth WK 1993. Quantitative effects of grazing on vegetation and soil over a global range of environments. Ecological Monographs 63: 327–366.

Milchunas DG, Varnamkhasti AS, Lauenroth WK and Goetz H 1995. Forage quality in relation to long-term grazing history, current-year defoliation, and water resource. Oecologia 101: 366-374.

Milchunas DG and Noy-Meir I 2002. Grazing refuges, external avoidance of herbivory and plant diversity. Oikos 99: 113-130.

Milliken GA and Johnson DE 1992. Analysis of Messy Data 2nd ed Vol 1 Chapman and Hall, New York.

Moleele NM and Perkins J 1998. Encroaching woody plant species and boreholes: is cattle density the main driving factor in the Olifants Drift communal grazing lands, Botswana? Journal of Arid Environments 40: 245-253.

Mueller-Dombois D and Ellenberg H 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons, New York.

Negi GCS, Rikhari HC and Singh SP 1993. Plant regrowth following selective horse and sheep grazing and clipping in an Indian Central Himalayan alpine meadow. Artic and Alpine Research 25: 211-215.

Norton BW 1981. Differences between species in forage quality. In: Hacker JB (ed) Nutritional Limits to Animal Production from Pastures. Commonwealth Agricultural Bureaux. Farnham Royal, UK. pp. 89–110.

Noy-Meir I 1993. Compensation growth of grazed plants and its relevance to the use of rangelands. Ecological Applications 31: 32-34.

O'Connor TG 1991. Local extinction in perennial grasslands: a life history approach. American Naturalist 137: 753-773.

Oesterheld M and McNaughton SJ 1988. Intraspecific variation in response of *Themeda triandra* to defoliation – the effects of time of recovery and growth rates on compensatory growth. Oecologia 77: 181-186.

Parris R and Child G 1973. The importance of pans to wildlife in the Kalahari and the effects of human settlement on these areas. Journal of South African Wildlife Management Association 3: 1-8.

Penning de Vries FWT and Djtèye MA 1982. La productivitè des pasturages Sahèliens. Centre for Agricultural Publishing and Documentation, Wageningen.

Reid RL and Horvath DJ 1980.Soil chemistry and mineral problems in farm livestock: A review. Animal Feed Science and Technology 5: 95-167.

Ritchie ME, Tilman D and Knops JMH 1998. Herbivory effects on plants and nitrogen dynamics in oak savanna. Ecology 79: 165-177.

Rosenthal JP and Kotanen PM 1994. Terrestrial plant tolerance to herbivory. Trends in Ecology and Evolution 9: 145-148

Ross DJ and Tate KR 1984. Microbial biomass in soil: effects of some experimental variables on biochemical estimations. Soil Biology and Biochemistry 16: 161-167.

Russell GEG, Watson L, Koekemoer M, Smook L, Barker NP, Anderson HM and Dallwitz MJ 1991. Grasses of southern Africa. Botanical Research Council, South Africa.

Shapiro SS, Wilk MB and Chen HJ 1968. A comparative study of various tests of normality. Journal of the American Statistical Association 63: 1343-1372.

Smet M and Ward D 2005. A comparison of the effects of different rangeland management systems on plant species composition, diversity and vegetation structure in a semi-arid savanna. African Journal of Range and Forage Science 22: 59-71.

Stark S, Strommer R and Tuomi J 2002. Reindeer grazing and soil microbial processes in two suboceanic and two subcontinental tundra heaths. Oikos: 97: 69-78.

StatSoft, Inc. 2002. STATISTICA for Windows [Computer programme manual]. StatSoft, Inc, Tulsa, OK, USA.

Tomlinson KW, Hearne JW and Alexander RR 2002. An approach to evaluate the effect of property size on land-use options in semi-arid rangelands. Ecological Modelling 149: 85-95.

Turner CL, Seastedt TR and Dyer MI 1993. Maximization of aboveground grassland production: The role of defoliation frequency, intensity, and history. Ecological Applications 3: 175-186.

Van Oudtshoorn F 1999. Guide to grasses of southern Africa. Briza Publication, Pretoria, South Africa.

Van Riet and Louw Landscape Architects and Metaplan 1999. Kimberley Triangle Community Resource Project. The Kimberley Triangle Forum, Phases one to seven. Pretoria. 53 pp.

Van Soest PJ 1994. Nutritional Ecology of the Ruminant (2 nd edn). Comstock Publishing Associates, London.

Varnamkhasti AS, Milchunas DG, Lauenroth WK and Goetz H 1995. Production and rain use efficiency in short-grass steppe: grazing history, defoliation and water resource. Journal of Vegetation Science 6: 787-796.

Ward D 2004. Ecological, historical and social perspectives on rangeland degradation in arid communal rangelands in Namibia. In: Vetter S (ed) Rangelands at equilibrium and non-equilibrium: Recent developments in debate around rangeland ecology and management. Programme for Land and Agrarian Studies, Cape Town, South Africa pp 37-40.

Ward D, Ngairorue BT, Kathena J, Samuels R and Ofran Y 1998. Land degradation is not a necessary outcome of communal pastoralism in arid Namibia. Journal of Arid Environments 40: 357-371.

Ward D, Saltz D, Rowen M and Schmidt I 1999. Effects of grazing by re-introduced *Equus hemionus* on the vegetation in a Negev desert erosion cirque. Journal of Vegetation Science 10: 579-586.

Ward D, Saltz D, and Ngairorue BT 2004. Spatio-temporal rainfall variation and stock management in arid Namibia. Journal of Range Management 57: 130-140.

Whitehead DC 2000. Nutrient elements in grassland: Soil - plant – animal relationships. CABI Publishing, Wallingford, UK.

Wilms WD, Dormaar JF, Adams BW and Douwes HE 2002. Response of the mixed prairie to protection from grazing. Journal of Range Management 55: 210–216.

Wolfson MM 1999. The response of forage plants to defoliation: Grass. In: NM Tainton (ed), Veld Management in South Africa. University of Natal Press, Pietermaritzburg, South Africa. pp 91-103.

Wolfson MM and Tainton NM 1999. The morphology and physiology of the major forage plants. In: Tainton NM (ed) Veld Management in South Africa. University of Natal Press, Pietermaritzburg, South Africa. pp 54-79.

Zacharias PKJ 1986. The use of the cellulase digestion procedure for indexing the dry matter digestibility of forage. Journal of the Grassland Society of Southern Africa 3: 117-121.

Chapter 5

Using faecal profiling to assess the effects of different management types on diet quality in semi-arid savanna

Abstract

We used faecal profiling to assess diet quality of animals under three different management types in a semi-arid savanna, northwest of Kimberley, Northern Cape, South Africa. The levels of faecal crude protein (FCP) and faecal phosphorus (FP) of free-ranging springbok, *Antidorcas marsupialis* and blue wildebeest, *Connochaetes taurinus* on a game ranch goats and cattle grazing in a communally-managed area as well as cattle grazing under commercial management were determined in the wet and dry seasons over a period of two years. Plant and soil analyses were also conducted. Goats had the highest FCP and FP of all species in all seasons during the study. It appeared that selective feeders (goats and springbok) and short-grass feeders (wildebeest) do not suffer from low forage quality because their FCP and FP levels were above critical values during all seasons. Contrastingly, cattle need nutrient supplementation because their FCP and FP were below critical nutritional values during the dry seasons. Plant and soil chemical characteristics, especially soil P, had an influence on faecal quality during the study. Clay pans provide an important habitat because of the high soil quality and, consequently, high diet quality. Our surprising finding that faecal CP levels were higher under communal management than under commercial management may be ascribed to higher nutrient deposition (due to higher stocking rates) and greater diet selectivity available to free-ranging animals under communal management. Higher faecal CP and P levels in game animals may also be ascribed to unrestricted movement and, consequently, greater access to palatable plants. The results of this study demonstrate the value of faecal profiling for management of semi-arid savanna livestock and game.

Keywords: diet quality**,** crude protein, phosphorus, faeces, management types

---

Accepted for 2006 African Journal of Range and Forage Science 23: 29-38.

Introduction

Diet quality is perhaps the most important factor influencing animal production on natural grazing lands (Wilson 1982). In natural veld, forage resources vary in their quality, space and time (Robbins 1993, Caughley and Sinclair 1994, Van Soest 1994, Knapp *et al.* 1999) resulting in seasonal changes in diet quality, accessibility and availability (Kiringe *et al.* 1999). Diet quality varies with the proportion of the particular plant species consumed. Mammalian herbivores seldom obtain the best possible diet from a single plant and must optimise their nutritional and energy needs by selection of a series of food resources with complementary concentrations of nutrients (Freeland and Janzen 1974, Belovsky 1981, Robbins 1993). Consequently, nutrient levels of collected forages are generally unreliable for determining diet quality of free-ranging animals (Holechek *et al.*1982a, Grant *et al.* 2001) because ungulates have the ability to select the most nutritious plants or plant parts available (Krueger 1972, Belovsky 1981, Howery and Pfister 1990, Irwin *et al.* 1993).

Many methods have been used in the past to determine the quality of herbivore's diet but they suffer a variety of problems. Direct field observations are tedious and it is also difficult to assess the exact proportions of each plant species consumed because of variation in bite size. Fistulation is a more direct but invasive, costly and ethically questionable technique for assessing diet quality (Wrench *et al.* 1997) and oesophageal fistulation is impractical for free-ranging animals. Moreover, it is unsuitable for dietary phosphorus assessment because of salivary phosphorus contamination (Holechek *et al.* 1985). This limits its practical application for large number of animals over extended time periods. Contrastingly, using faecal samples for assessing diet quality is easy and inexpensive (Mould and Robbins 1981, Wofford *et al.* 1985, Grant *et al.* 1995). Faecal indices of diet quality, such as those using CP and P, have shown to be a useful tool.

Faecal crude protein and phosphorus

Protein is a limiting nutrient for herbivores; hence, dietary protein can predict nutritional status (Milford and Minson 1965). Crude protein in faeces has been shown to positively correlate with crude protein concentration of dietary feed in a number of studies (Mould and Robbins 1981, Holechek *et al*. 1982a, Grant 1989, Grant *et al.* 1995, Wrench *et al.* 1997). In mature ruminants, faecal crude protein concentration is also closely related to dietary intake (Arnold and Dudzinski 1978, Grant 1989), dietary dry matter digestibility (Leslie and Starkey 1985) and live mass changes (Gates and Hudson 1981, Grant *et al.* 1996). Moreover, faecal crude protein is positively correlated with changes in dietary phosphorus (Holechek *et al.* 1982a, 1982b, Leslie and Starkey 1985, Irwin *et al.* 1993).

Faecal CP has limitations, largely because faecal CP in browsers and mixed-feeders can be unusually elevated (Mould and Robbins 1981) due to the protein-precipitating effects of tannins (Hagerman and Butler 1981), although this is not a problem for grazers (Ellis 1990, Chesselet *et al.* 1992, Irwin *et al.*1993). Thus, faecal CP is a good indicator of diet quality for grazers but is not necessarily so for browsers and mixed-feeders. Faecal P also reflects dietary P (Belonje 1980, Holechek *et al.* 1985, Betteridge and Andrews 1986, Karn 1997) and is consistent among all feeding styles, i.e. browsers, grazers and mixed-feeders. Phosphorus is a limiting mineral, and low soil P leads to low plant P (Vallentine 2001) and, hence, low P in the diet.

Management implications

Sound knowledge of changes over time in the major minerals and nutrients in the veld can help to optimise stocking densities and avoid stock losses related to lack of these substances (Stuth *et al*. 1999). If faecal profiling is used regularly, ranch managers can also estimate whether current minerals added in the diet are meeting the threshold requirements for minerals (Stuth *et al*. 1999). Furthermore, when faecal crude protein and phosphorus fall below nutritional thresholds for a long time, managers can use faecal profiling as a means of determining whether destocking is necessary.

The objective of this study was to determine veld quality and diet quality of different mammalian herbivores grazing under different management types in a semi-arid savanna using faecal profiling. The seasonal variation of CP and P levels in cattle, goats, *Antidorcas marsupialis* (springbok), and *Connochaetes taurinus* (blue wildebeest) were examined in commercial, communal and game management types on a single large estate in the Northern Cape, South Africa, facilitating comparison of differences in diet quality among management types under similar habitat conditions. The relationships between seasonal plant quality and seasonal faecal quality were also assessed.

Materials and methods

Study area and vegetation

This study was conducted on Pniel Estates (21 000ha) situated in the Northern Cape Province, South Africa, located at 28º 36' S, 24º 32' E, 1 124m. Pniel Estates consists of a game ranch (7 000ha), a commercial cattle ranch (11 000ha) and a communal ranch (3 000ha). The close proximity of these ranches and the similarity in soil type facilitate comparison of the impacts of game, communal and commercial management types on forage quality and quantity in semi-arid savanna. Mean stock number on the game area was 10.965ha LSU^{-1}, on the communally-managed area was 9.375ha LSU^{-1} and 16ha LSU^{-1} on the commercial area (Smet and Ward 2005).

The vegetation type in this semi-arid savanna is known as Kimberley Thorn Bushveld (Low and Rebelo 1998) or Kalahari Thornveld (Acocks 1988). In all management types, there is a rocky habitat type, which is characterized by andesite rocks with short grasses, forbs and shrubs (mostly *Acacia mellifera*). *Heteropogon contortus, Enneapogon scoparius, Enneapogon. desvauxii, A. congesta* and *E. obtusa* were more frequently observed in the rocky habitat than in other habitats.The soil type is mainly sandy loam.

Open savanna is also found in all management types. *Acacia erioloba* trees forms most of the overstory and the understory consists of a wide diversity of grasses and herbaceous plants in sandy soil. Under *A. erioloba,* there are usually shrubs such as *A. tortilis, Lebeckia linearifolia, Grewia flava, Lycium bosciifolium, L. hirsutum, Tarchonanthus camphoratus* and *Ziziphus mucronata.* The dominant perennial grass species in the present in open savanna were *Schmidtia pappophoroides*, *Eragrostis lehmanniana, Pogonarthria squarrosa* and *Aristida congesta*.

The game ranch has two more habitats that do not exist in the other management types, namely shrub and pans. Mostly *T. camphoratus*, *G. flava*, different grass species and herbaceous plants in sandy clay soil characterize the shrubby habitat. Pans have vegetation that differs in species and life form composition from the surrounding savanna (Parris and Child 1973) as all plant species are dwarfed. This habitat is seasonally inundated and has dark clay soil. In our study area, the dominant grasses in the clay-pan habitat, *Cynodon dactylon, E. lehmanniana* and *E. obtusa*, are perennials. Apart from these three grass species, *M. incanum* and *A. bechuanicus* and *Pentzia* species (especially *P. incana),* and karooid shrubs (often associated with the Karoo region of South Africa) are dominant species found on the clay pans.

Climate and soil

The study area is in the summer rainfall area in South Africa. The mean annual rainfall for nearby Barkly West is 388mm; rainfall among years is extremely variable (C.V. = 39%) (Kraaij 2002). Most rain occurs in the form of thunderstorms between January and March, with very little rain between May and October. The temperature varies between -8°C to 41°C, with a mean of 19°C (Low and Rebelo 1998). Daily maximum temperatures exceed 30 °C in summer, while for the remainder of the year the days are warm, and the nights in winter are very cold (Van Riet and Louw 1999). During the study period from January 2001 to January 2004, the annual rainfall (Figure 5.1) was 29% above mean rainfall in 2000/2001; was 21% below average in 2001/2002 and in 2002/2003 was 72% below average (severe drought).

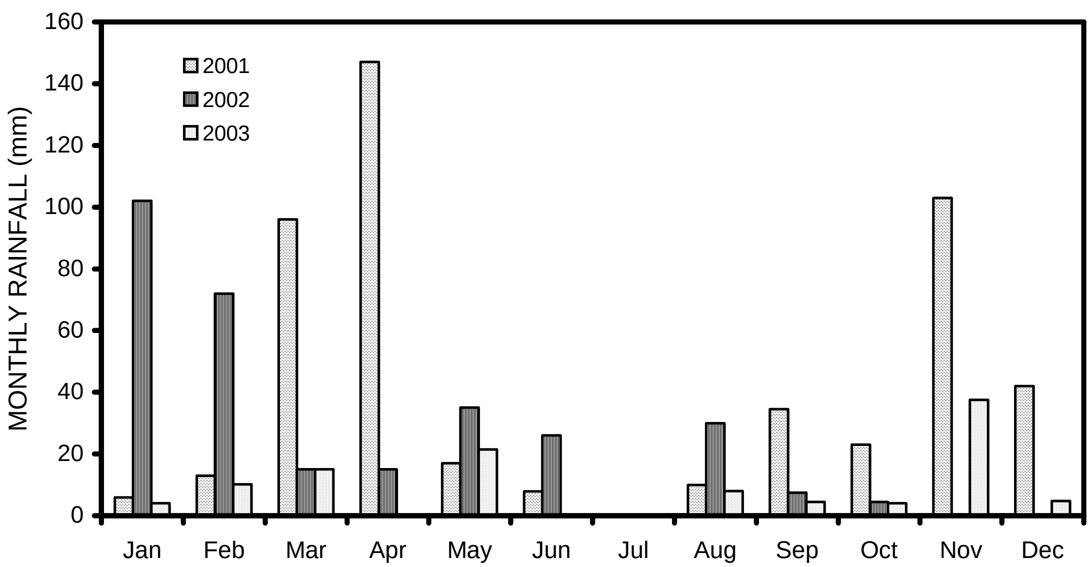

Figure 5.1: Distribution of monthly rainfall at Barkly West during the study period (2001-2003)

Most soils are leached or calcareous due to the hot dry conditions (Low and Rebelo 1998). The soils consist of a thin layer of light brown sandy loam that is underlaid by either hard limestone or hard sand loam.

The soil type at Pniel varies from moderately deep (0.3 – 0.6m) to deep (> 0.6m) red and yellow sands (Hutton, Clovelly and Kimberley soil forms) to shallow (< 0.3m) and stony (Mispah, Prieska and Glenrosa soil forms) (Bezuidenhout 1995). Sandy soils can be up to 8m deep (Van Riet and Louw 1999). The physical characteristics of soils make them unsuitable for crop cultivation; consequently, game and livestock ranching are mostly practised in the area.

Field Experiments

Sampling plots

Six unfenced plots were randomly-selected in rocky and open savanna habitat types in each management type (game, communal and commercial) with the exception of open savanna habitat type in commercial management type, which had eight because of the greater size of this habitat. This resulted in 38 experimental plots. In addition to these 38 experimental plots, six plots in shrubby and six plots in pan habitat types of the game management type were added. At the end we had 50 experimental plots for the study. We used a Global Positioning System and poles to mark all plots.

Soil sampling

Two randomly-selected soil samples were collected in each of the above-mentioned plots and then combined to form one composite soil sample for each plot. Core soil samples were collected from the top 20cm of soil after the surface-plant debris and stones were removed.

Plant nutritional measurements

Grass height was measured in all plots in the 2002 wet season, 2002 dry season, 2003 wet season, 2003 dry season and 2004 wet season using a point frequency frame (Mueller-Dombois and Ellenberg 1974). We could not collect data in the early dry season because this season coincides with the hunting season, when access was restricted for safety reasons. The point-frequency frame (also called a “Levy bridge”) is a quick and effective method of estimating plant height, species composition and percentage cover (Mueller-Dombois and Ellenberg 1974).

To convert mean plant height values to biomass, we regressed plant height values on biomass assessed from a sub-set of samples in each plot. A 1m x 1m grid was placed over the Levy bridge in each plot and vegetation within the grid was clipped as close to the ground as possible. This was repeated three times in each plot. Aboveground biomass was calculated as the sum of the biomass of live and green plants as well as standing dead plant material. Clipped plant samples were oven dried at 60ºC to constant mass and then weighed to estimate plant dry weight.

Faecal sample collection

Fresh faecal samples were collected in the 2002 wet season, 2002 dry season, 2003 wet season, 2003 dry season and 2004 wet season from all management types and ensuring that samples were not contaminated with soil, fungi and insects (Jenks *et al.* 1990, Wrench *et al.* 1996). Date of collection, animal species, and management type were noted for all faecal samples collected. Faeces were collected for grazers and mixed-feeders. In the communal area, cattle represented grazers and goats represented mixed-feeders although there were a few other domestic animals. Cattle are the only animals kept in the commercially-managed area. In the game ranch there were a number of wild ungulates, but springbok, a mixed-feeder, and blue wildebeest, a grazer, were selected as the most common representatives of these two feeding types for data collection. To obtain a representative sample, at least five different faecal samples of each animal species were collected in each sampling period. Faecal samples of juvenile, pregnant and lactating animals were avoided (by direct observation of defaecating animals).

Laboratory analyses

Soil characteristics

All the soil samples were air dried and sieved through a 2mm mesh size. These samples were tested for the presence of inorganic carbon in the form of $CaCO_3$ by adding concentrated hydrochloric acid according to the method of Nelson and Sommers (1982). Thereafter, soil samples were analysed for pH, conductivity and percentage organic carbon. Soil pH was measured by mixing the soil sample with a water solution in a ratio of 1:5 soil:water (according to Brinkley and Vitousek 1996) using a Corning pH meter 430. Soil conductivity was determined in a 1:5 soil:water ratio saturation extract (Rhoades 1982) using a Corning conductivity meter 441. Organic carbon content was determined using the Walkley-Black method (Nelson and Sommers 1982). This method was used to avoid misinterpretation of organic carbon due to the presence of inorganic carbon in the form of carbonate in calcareous soil. Soil total nitrogen was measured using Dumas' total combustion method (Bremner 1996) with a LECO FP-528 nitrogen analyser. Available phosphorus (P) was analysed using the Bray II method (Bray and Kurtz 1945). Water-holding capacity of soil was determined through comparisons of the volume of water contained in each soil type at saturation level (Rhoades 1982).

Nutritional characteristics of plants

Crude protein (CP) of plant concentrations was determined using a standard Kjeldahl technique (AOAC 1990). Phosphorus concentrations were ascertained spectrophotometrically according to the micro technique of the AOAC (1990). The high fibre content of certain grass species reduces the nutritional value to animals in spite of relatively high energy and protein contents. Hence, the dry matter digestibility of grass species was indexed by the *in vitro* digestible dry matter method of Zacharias (1986) because this technique incorporates concentrations, ratios and structures of forage constituents in an index of potential for breakdown by rumen microbial populations (Milchunas *et al.* 1995).

Faecal profiling

Faecal samples were stored in a well-aerated and dry place and then transported to the University of Stellenbosch laboratory. On arrival, they were immediately dried in an oven at 60ºC for 48 hours. Dried samples were ground in a mill to pass 0.5mm sieve and stored in sealed plastic containers at room temperature pending analysis. Faecal samples were analyzed for crude protein (CP) by Kjeldahl procedure (AOAC 1990).

Phosphorus concentration was determined using a standard technique (AOAC 1990) by spectrophotometer at 650nm wavelength.

Statistical analyses

Normality of data distribution was confirmed by the Shapiro-Wilks' W test (Shapiro *et al.* 1968, StatSoft 2002). Analysis of variance of seasonal differences in faecal nutritive levels for animals in various managements, grazers and mixed-feeders as well as differences among various animal species in Pniel Estates were conducted using a general linear model (GLM) procedure of *Statistica* (v.6, 1984-2004 Statsoft Inc.). Where necessary, data were transformed to meet the requirements of parametric analyses. Scheffe *post hoc* comparisons of means were performed on plant and faecal CP and P and all soil chemical characteristics of different management types. Pearson product-moment correlation analyses were used for comparisons of plant CP and faecal CP; plant P and faecal P; as well as faecal CP and faecal P in different managements. Distributions were compared with Kolmogorov-Smirnov two-sample tests.

Results

Soil characteristics

There were no significant differences in soil conductivity ($F_{2, 47,}$ = 1.59, P = 0.21) and pH ($F_{2, 47}$ = 048, P = 0.62) among management types (Table 5.1). Management type had a significant effect ($F_{2, 47}$ = 3.88, P = 0.03) on soil N, on soil P ($F_{2, 47}$ = 4.21, P = 0.02), on soil water-conductivity ($F_{2, 47}$ = 3.34, P = 0.04) and on soil organic carbon ($F_{2, 47}$ = 3.26, P = 0.04) (Table 5.1). The game management type had significantly higher levels of soil N and soil P than the other management types (Scheffe *post hoc* test, p < 0.05).

Forage nutritional quality

Dry matter digestibility

In vitro dry matter digestibility showed no significant differences (range in P = 0.11 – 0.64) among management and habitat types during the study. In the wet seasons, the mean in vitro dry matter digestibility ranged between 49.59 – 58.82% and between 35.92-47.80% in the dry seasons.

Crude protein (CP) content

Significant effects ($F_{2, 47}$ = 3.92, P = 0.03 and $F_{2, 42}$ = 4.24, P = 0.02) of management types were observed on plant CP content of the wet and the dry seasons of 2002, respectively (Table 5.2). In the dry season of 2002, communal management type showed significantly higher plant CP levels than in commercial management (Scheffe *post hoc* test, p < 0.05). Management types had no significant effects ($F_{2, 46}$ = 0.389, P = 0.96; $F_{2, 42}$ = 1.56, P = 0.22 and $F_{2, 47}$ = 0.63, P = 0.54) on plant CP levels in the wet and the dry seasons of 2003, as well as in the wet season of 2004, respectively (Table 5.2).

Table 5.1: Effects of management type on soil organic carbon, nitrogen, phosphorus, pH, water-holding capacity and conductivity levels (mean ± SE) in Pniel Estates

Parameter	Management	n	Mean ± SE
Organic carbon (%)	Communal	12	0.68 ± 0.081
	Game	24	0.86 ± 0.06
	Commercial	14	0.62 ± 0.08
Nitrogen (%)	Communal	12	0.04 ± 0.01
	Game	24	0.06 ± 0.003
	Commercial	14	0.05 ± 0.005
Phosphorus (mg/kg)	Communal	12	5.98 ± 8.22
	Game	24	26.77 ± 5.81
	Commercial	14	6.70 ± 7.61
pH	Communal	12	5.74 ± 0.19
	Game	24	5.86 ± 0.14
	Commercial	14	5.65 ± 0.17
Water- holding capacity (%)	Communal	12	31.39 ± 1.86
	Game	24	36.58 ± 1.31
	Commercial	14	31.57 ± 1.72
Conductivity (μS/cm)	Communal	12	48.99 ± 8.38
	Game	24	57.11 ± 5.92
	Commercial	14	39.75 ± 7.76

Phosphorus (P) content

Management types had a significant effect ($F_{3, 45} = 18.86$, $P < 0.001$) on plant P content in the wet season of 2003 only (Table 5.2). During this wet season, game management type had significantly higher forage P content than in commercial management (Scheffe *post hoc* test, $p < 0.05$). Non-significant effects of management types on plant P levels were observed ($F_{2, 47} = 1.17$, $P = 0.32$; $F_{2, 42} = 0.38$, $P = 0.68$; $F_{2, 46} = 0.69$, $P = 0.51$ and F = $_{2,47}$ = 1.19, $P = 0.31$) in the 2002 wet and dry season as well as the dry season of 2003 and 2004 wet season, respectively (Table 5.2).

Table 5.2: Mean values of plant CP and P concentrations (% ± SE) among management types during the wet and dry seasons on Pniel Estates over two years (Jan 2002 – Jan 2004)

Year	Season	Management type	n	CP (%)	P (%)
2002	Wet	Game	24	5.89 ± 0.29	0.09 ± 0.006
		Communal	12	7.09 ± 0.41	0.09 ± 0.009
		Commercial	14	6.91 ± 0.38	0.08 ± 0.008
2002	End of dry	Game	16	7.12 ± 0.24	0.10 ± 0.007
		Communal	9	7.07 ± 0.32	0.08 ± 0.01
		Commercial	14	5.58 ± 0.25	0.06 ± 0.009
2003	Wet	Game	24	8.91 ± 0.21	0.12 ± 0.005
		Communal	11	8.91 ± 0.32	0.10 ± 0.007
		Commercial	14	8.88 ± 0.28	0.09 ± 0.006
2003	End of dry	Game	23	6.95 ± 0.34	0.05 ± 0.005
		Communal	11	6.34 ± 0.49	0.05 ± 0.007
		Commercial	14	6.18 ± 0.44	0.04 ± 0.007
2004	Wet	Game	24	10.93 ± 0.49	0.11 ± 0.005
		Communal	12	11.25 ± 0.69	0.11 ± 0.008
		Commercial	14	10.27± 0.62	0.09 ± 0.007

Faecal quality

Faecal CP

Faecal CP level differed significantly ($F_{2, 33} = 4.61$, $P = 0.017$) among management types in the wet season of 2002 (Table 5.3). Commercial management had significantly lower faecal CP content than other management types. Similarly, there was a significant difference among management types ($F_{2, 29} = 3.28$, $P = 0.049$ and $F_{2, 39} = 8.79$, $P < 0.001$) in faecal CP content in the wet seasons of 2003 and 2004, respectively (Table 5.3). Also, a significant influence ($F_{2, 25} = 3.39$, $P = 0.046$ and $F_{2, 28} = 3.36$, $P = 0.04$) of management type was observed in the dry seasons of 2002 and 2003, respectively (Table 5.3). Communal management type had a higher faecal CP level than other management types in most seasons. Across seasons, there was a positive and significant correlation between plant CP and faecal CP levels ($r = 0.6$, $P = 0.049$).

In the wet season of 2002 there was a significant difference ($F_{4, 40} = 58.73$, $P < 0.001$) in faecal CP content among animal species (Table 5.4). Goats had significantly higher faecal CP than other animal species and faecal CP of springbok was significantly higher than that of cattle grazing in communal and commercial areas and wildebeest. A highly significant influence ($F_{4, 34} = 37.12$, $P < 0.001$) of animal species was observed on faecal CP concentrations in the dry season of 2002. Similarly, a significant difference ($F_{4, 30} = 5.04$, $P = 0.004$; $F_{4, 26} = 4.44$, $P = 0.007$ and $F_{4, 37} = 32.52$, $P < 0.001$) in faecal CP levels were observed among animal species in the wet season of 2003, the dry season of 2003 and the wet season of 2004, respectively (Table 5.4). Goats had significantly higher concentrations of faecal CP level than other animal species in all seasons (Scheffe *post hoc* test, $p < 0.05$). Similarly, springbok had a significantly higher faecal CP level than cattle and wildebeest.

Table 5.3: Mean faecal CP and P (% ± SE) of different management types in the wet and end of dry seasons on Pniel Estates during 2002-2004

Year	Season	Management type	CP (%)	P (%)
2002	Wet	Game	11.66± 0.85	0.49 ± 0.38
		Communal	11.49 ± 0.60	0.31 ± 0.03
		Commercial	8.56 ± 0.85	0.24 ± 0.04
2002	End of dry	Game	7.85 ± 1.12	0.25 ± 0.05
		Communal	10.02 ± 0.56	0.28 ± 0.03
		Commercial	7.88 ± 0.79	0.19 ± 0.04
2003	Wet	Game	9.24 ± 0.49	0.30 ± 0.02
		Communal	10.17 ± 0.52	0.27 ± 0.02
		Commercial	8.18 ± 0.57	0.21 ± 0.03
2003	End of dry	Game	8.05 ± 0.42	0.21 ± 0.03
		Communal	9.37 ± 0.52	0.20 ± 0.03
		Commercial	6.76 ± 1.01	0.20 ± 0.06
2004	Wet	Game	10.22 ± 0.41	0.40 ±0.02
		Communal	12.77 ± 0.45	0.30 ± 0.02
		Commercial	11.16 ± 0.68	0.26 ± 0.03

Faecal P

Management type had a significant influence ($F_{2, 33} = 16.39$, $P < 0.001$ and $F_{2, 29} = 3.42$, $P = 0.04$) on faecal P levels in the wet seasons of 2002 and 2003, respectively (Table 5.3). Game management had significantly higher faecal P levels than in other management types (Scheffe *post hoc* test, $p < 0.05$). A non-significant difference ($F_{2, 25} = 1.89$, $P = 0.17$; $F_{2, 28} = 0.079$, $P = 0.92$ and $F_{2, 39} = 2.10$, $P = 0.14$) in faecal P concentration among management types was observed in the dry season of 2002 and 2003 as well as in the wet season of 2004, respectively (Table 5.3).

Faecal P levels were significantly different ($F_{4, 40} = 29.69$, $P < 0.001$; $F_{4, 27} = 6.28$, $P = 0.001$ and $F_{4, 37} = 4.87$, $P = 0.003$) among animal species in the wet seasons of 2002, 2003 and 2004, respectively (Table 5.4). Similarly, in the dry season of 2002, there was a significant difference ($F_{4, 34} = 36.13$ $P < 0.001$) in faecal P level among animal species, with goats showing higher faecal P than other animal species (Scheffe *post hoc* test, $p < 0.05$). Contrastingly, a non-significant difference ($F_{4, 30} = 0.89$, $P = 0.48$) among animal species in faecal P level was recorded in the dry season of 2003. A significant and positive correlation between plant P and faecal P levels was observed ($r = 0.6$, $P = 0.03$).

Table 5.4: Effects of management type on faecal CP and P concentrations of different animals (mean (%) ± SE) on Pniel Estates

Year	Season	Animal species	n	CP (%)	P (%)
2002	Wet	Blue wildebeest	9	10.48 ± 0.59	0.309 ± 0.03
		Goat	8	15.38 ± 0.43	0.43 ± 0.03
		Commercial cattle	9	8.56 ± 0.38	0.20 ± 0.03
		Communal cattle	11	9.01 ± 0.35	0.22 ± 0.03
		Springbok	9	11.66 ± 0.38	0.49 ± 0.03
2002	End of dry	Blue wildebeest	7	8.86 ± 054	0.30 ± 0.02
		Goat	7	12.84 ± 0.41	0.41 ± 0.02
		Commercial cattle	8	7.89 ± 0.38	0.19 ± 0.02
		Communal cattle	8	7.82 ± 0.36	0.20 ± 0.02
		Springbok	9	9.16 ± 0.34	0.34 ± 0.02
2003	Wet	Blue wildebeest	7	9.53 ± 0.61	0.29 ± 0.03
		Goat	7	11.82 ± 0.67	0.36 ± 0.03
		Commercial cattle	9	8.18 ± 0.51	0.21 ± 0.02
		Communal cattle	8	8.79 ± 0.61	0.20 ± 0.03
		Springbok	7	8.96 ± 0.61	0.31 ± 0.03
2003	End of dry	Blue wildebeest	8	8.07 ± 0.55	0.23 ± 0.04
		Goat	7	10.68 ± 0.63	0.26 ± 0.04
		Commercial cattle	7	6.76 ± 0.89	0.19 ± 0.06
		Communal cattle	6	7.81 ± 0.69	0.17 ± 0.05
		Springbok	9	8.03 ± 0.52	0.18 ± 0.04
2004	Wet	Blue wildebeest	9	9.85 ± 0.35	0.29 ± 0.03
		Goat	8	15.05 ± 0.37	0.35 ± 0.03
		Commercial cattle	7	10.16 ± 0.39	0.26 ± 0.02
		Communal cattle	8	10.50 ± 0.37	0.24 ± 0.03
		Springbok	10	10.57 ± 0.33	0.38 ± 0.02

Discussion

Effects of management types

Soils in the game section of Pniel Estates were of higher overall quality than under other management types (Tables 5.1). The high quality of soil in this area is reflected in better overall forage quality than in other management types. This is largely due to the fact that the pan habitat type had the highest soil quality and only occurred in the game management type (Mbatha and Ward in prep). Surprisingly, the communal area had the highest plant CP levels in all seasons, except in the 2002 wet season when the highest plant CP content was observed in the game area (Ward *et al*. 2000). This resulted in higher faecal CP content of goats and cattle in the communally-managed area than under commercial management. This occurred despite the fact that the communally-managed area had the lowest level of soil nitrogen. The high faecal CP level in animals on the nutrient-poor sandy soil in the communal area is similar to the results observed by Grant *et al.* (2001) in the Mpumulanga lowveld (South Africa) where animals on nutrient-poor granite soil had higher faecal CP content than on more nutrient-rich soils. Thus, plant CP level was associated with high faecal CP in spite of low soil CP content. This can be attributed to more faecal and urine deposition due to higher stocking densities observed in the communal area (see Ward *et al*. 1998, Mbatha and Ward in prep) and, perhaps, to greater diet selectivity available to free-ranging animals under communal management (rotational grazing under commercial management may restrict access to the most palatable plants at certain times of year).

Faecal P below 0.2% is considered to be indicative of P limitation (Dörgeloh *et al*. 1998). In our study, faecal P never dropped below 0.2% in any management type in any period. Additionally, we found that faecal P increased in the wet seasons and the highest inter-annual faecal P levels were detected in the year when rainfall was the highest. These results are consistent with results of previous studies that showed that phosphorus uptake by plants is positively correlated with soil moisture (Reid and Horvath 1980, Scholes and Walker 1993, McDonald *et al.* 1996). During the study, in all management types, quality of dry and dead plants was low, and limited forage was available, which was coupled with low plant P concentrations, which is similar to observations by Underwood and Suttle (1999). This resulted in non-significant differences in faecal P level among management types. These results accord with observations by Grant *et al.* (1996). A significant difference in faecal P levels among different management types during the wet seasons reflects a difference in dietary quality.

Differences among animal species

There was a significant difference in faecal CP among animal species during the whole study period; goats had the highest faecal CP levels. Mixed-feeders usually have small mouths and can easily select forage with higher nutritive value compared to what is randomly available on the ranch (Hofmann 1989, Shipley 1999, Gagnon and Chew 2000). Additionally, they can switch to high-quality browse when grass quality is low (Shipley 1999, Mbatha 2001). The higher level of faecal CP in goats could be attributed to year-round browsing (browse typically has higher levels of CP than grass) in semi-arid savanna (Bergström and Skarpe 1999). The other mixed-feeder in this study, springbok, grazes on short grass in the wet season and browses on dwarf shrubs surrounding the pans in the dry season (Bigalke 1972). Not surprisingly, therefore, mixed-feeders (goats and springbok) had higher faecal CP content than the grazers in this study (cattle and blue wildebeest). We note that higher levels of CP in the diet of mixed-feeders occurred in spite of high tannin levels (a known antifeedant) in many browse species of this area (Cooper and Owen-Smith 1985, Owen-Smith and Cooper 1987). The high faecal CP concentrations of mixed-feeder could be associated with protein-precipitating effect of tannins and not necessarily because more protein was ingested. However, the fact that the faecal P of mixed-feeders was also high indicates that these animal species selected a higher quality diet.

A significant difference in faecal CP among grazers was observed in the wet seasons only. This is possibly due to high grass quality in the wet season (Mbatha and Ward in prep). Thus, in the wet season, animals are able to select forage of the highest quality available, but species differ in their abilities to acquire high quality diets. During the dry season, all grazer species are faced with low quality forage, resulting in non-significant differences in faecal CP among grazer species. Among grazers, it was observed that faecal CP of blue wildebeest was higher than that of cattle in communal and commercial management types. Although blue wildebeest eat grasses only, they are highly selective for leaf blades year-round and prefer short grass with high nutrient quality (Owaga 1975, Sinclair 1974, Skinner and Smithers 1990). Therefore, harvesting behaviour and preference of short grass by blue wildebeest contributed to higher faecal CP than in cattle. Moreover, the game area has no fences and animals can freely graze wherever the forage quality is high. In our study, most grazers in the game areas were observed in the pans, which had the highest soil and plant quality among habitat types (Mbatha and Ward in prep).

The faecal CP content of all animal species tended to increase as the rainfall increased and the lowest faecal CP was observed when the rainfall was also very low (2002/2003 end of dry season). Faecal CP of cattle grazing in commercial area was 6.76 – 8.56% for most of the study period and was above 10% only once. The former is below the critical level of 8.75% as indicated by Wrench *et al*. (1997) to be associated with dietary CP deficiency for grazers on natural ranches. This level of faecal CP is above 7.19 – 7.5% required to maintain rumen fermentation (Grant *et al*. 1995).

Faecal P was significantly different among animal species in all wet seasons but not at the end of dry seasons. The significant difference in the wet season may be attributed to differences in selectivity among animal species. Goats and springbok had the highest faecal P levels in all wet seasons because they are able to choose plants (mostly shrubs and trees) with high P concentration almost throughout the year (Meissner *et al.* 1996). In the dry season, the nutritive value of grass and some herbaceous plants is low, mostly due to age (Reid and Horvath 1980, Norton 1981, McDowell 1996). Consequently, even the diet of selective feeders is of low quality, leading to a non-significant difference in faecal P in the dry seasons. Among grazers, blue wildebeest had a higher faecal P content than cattle, which can be attributed to both selective feeding on short-nutritious grass (see CP results above) and to higher soil P (and, thus, higher plant P) in the game area than in habitats occupied by cattle.

Conclusion and management implications

The most surprising finding in this study was that faecal quality was lowest in the commercial management type. We ascribe this to the higher nutrient deposition in communal management (due to higher stocking densities), thereby increasing soil quality, which affects plant quality in turn. An additional factor that may affect this result is that animals in communally-managed area have freedom of movement and may be better able to access high quality food items. We may interpret this to mean that a continuous grazing system may hold some advantages over a rotational system under these circumstances. If a rotational grazing system is designed such that all paddocks have the same proportional availability of key forage plants the differences we recorded should not occur because animals should be able to access preferred items in each camp. However, if key forage plants are patchily and unevenly distributed among paddocks, then managers may inadvertently be moving their animals to paddocks where lower overall diet quality is achievable. This points to the need for careful selection and distribution of paddocks and timing of movement of animals among paddocks.

The high faecal quality of animals in the clay pan habitat with high soil nutrients (see also Smet and Ward 2005, Britz 2004) shows that the pan habitat can be considered a key resource (Illius and O'Connor 2000). Indeed, game numbers in the pan habitat exceed those in other habitats, far in excess of the relative contribution on an area basis. These results demonstrate the importance of strategic planning of paddocks to incorporate this habitat in grazing systems in this region. Overall, our study shows that diet selectivity is a key factor in diet quality in semi-arid savanna. Consequently, assessing plant species availability is not particularly reliable method for assessing either habitat suitability or stocking rates. We recommend that faecal profiling, which explicitly incorporates diet selectivity, may be a more reliable method of managing these habitats.

References

Acocks JPH 1988. Veld Types of South Africa. Cape Town, Botanical Research Institute.

AOAC 1990. Official Methods of Analysis (15th edn). Association of Official Analytical Chemists, Washington DC, USA.

Arnold GW and Dudzinski ML 1978. Ethology of Free Ranging Animals Elsevier, New York.

Belonje PC 1980. The use of faecal analyses to estimate the phosphorus intake by grazing sheep. 1. The use of pool instead of individual samples. Onderstepoort Journal of Veterinary Research 47: 163-167.

Belovsky GE 1981. Food plant selection by a generalist herbivore: the moose. Ecology 62: 1020-1030.

Bergström R and Skarpe C 1999. The abundance of large wild herbivores in semi-arid savanna in relation to seasons, pans and livestock. African Journal Ecology 37: 12-26.

Betteridge K and Andrews WGK 1986. Intake and excretion of nitrogen, potassium and phosphorus by grazing steers. Journal of Agricultural Science 106: 393-404.

Bezuidenhout H 1995.An ecological study of the major vegetation communities of the Vaalbos National Park, Northern Cape. 2. The Graspan-Holpan section. Koedoe 38: 65-83

Bigalke RC 1972. Observations and feeding habits of the Springbok *Antidorcas marsupialis.* Zoologica Africana 7: 333-359.

Bray RH and Kurtz LT 1945. Determination of total, organic, and available forms of phosphorus in soils. Soil Science 59: 39-45.

Bremner JM 1996. Nitrogen-Total. In: DL Sparks, AL Page, PA Helmke, RH Loeppert, PN Soltanpour, MA Tabatabai, CT Johnston and ME Sumner (eds.), Methods of Soil Analysis. Part 3 Chemical Methods. American Society of Agronomy and Soil Science Society of America. Inc. Publisher. Madison, USA. pp 1085-1121.

Brinkley D and Vitousek P 1996. Soil nutrient availability. In: RW Pearcy J Ehleringer HA Mooney and PW Rundel (eds) Plant Physiological Ecology: Field Methods and Instrumentation (5th edn). Chapman and Hall, London. pp 75-96.

Britz M-L 2004. The effects of soil type and management strategy on vegetation structure and function in a semi-arid savanna, South Africa. MSc thesis, University of Stellenbosch, South Africa.

Caughley G and Sinclair ARE 1994. Wildlife Ecology and Management. Blackwell Scientific Publications, Boston.

Chesselet P, Wolfson MM and Ellis RP 1992. A comparative histochemical study of plant polyphenols in southern African grasses. Journal of the Grassland Society of Southern Africa 9: 119-125.

Cooper SM and Owen-Smith N 1985. Condensed tannins deter feeding by browsing ruminants in South African savanna. Oecologia 67: 142-146.

Dörgeloh WG, van Hoven W and Rethman NFG 1998. Faecal analysis as an indicator of the nutritional status of the diet of roan antelope in South Africa. South African Wildlife Research 28: 16-21.

Ellis RP 1990. Tannin-like Substances in Grass Leaves. Memoirs of the Botanical Survey of South Africa No 59. National Botanical Institute, South Africa.

Freeland WJ and Janzen DH 1974. Strategies in herbivory by mammals: The role of plant secondary compounds. The American Nature 108: 269-289.

Gagnon M and Chew AE 2000. Dietary preferences in extant African Bovidae. Journal of Mammalogy 81: 490-511.

Gates CC and Hudson RJ 1981. Weight dynamics of Wapiti in the boreal forest. Acta Theriologica 26: 467-518.

Grant CC 1989. Development of a system classifying and monitoring the availability of minerals to cattle in the ranching areas of S.W.A./Namibia. D.V.Sc. thesis. University of Pretoria, Pretoria, South Africa.

Grant CC, Meissner HN and Schultheiss WA 1995. The nutritive value of veld as indicated by faecal phosphorus and nitrogen and its relation to the condition and movement of prominent ruminants during the 1993-1993 drought in the Kruger National Park. Koedoe 38: 17-31.

Grant CC, Biggs HC, Meissner HH and Basson PA 1996. The usefulness of faecal phosphorus and nitrogen in interpreting differences in live-mass gain and the response to P supplementation in grazing cattle in arid regions. Onderstepoort Journal of Veterinary Science 2: 121-126.

Grant CC, Peel MJS, Zambatis N and van Ryssen JBJ 2001. Nitrogen and phosphorus concentration in faeces: an indicator of range quality as a practical adjunct to existing range evaluation methods. African Journal of Range and Forage Science 17: 81-92.

Hagerman AE and Butler LG 1981. The specificity of proanthocyanidin-protein interactions. Journal of Biological Chemistry 256: 4494-4497.

Hofmann RR 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: A comparative view of their digestive system. Oecologia 78: 443-457.

Holechek JL, Vavra M and Pieper RD 1982a. Methods for determining the nutritive quality of range ruminant diets: a review. Journal of Animal Science 54: 363-376.

Holechek JL, Vavra M and Arthun D 1982b. Relationships between performance, intake, diet nutritive quality and faecal nutritive quality of cattle on mountain range. Journal of Range Management 35: 741-744.

Holechek JL, Galyean ML, Wallace JD and Wafford H 1985. Evaluation of faecal indices for predicting phosphorus status of cattle. Grass and Forage Science 40: 489-492.

Howery LD and Pfister JA 1990. Dietary and faecal concentrations of nitrogen and phosphorus in penned white-tailed deer. Journal of Wildlife Management 54: 383-389.

Illius AW and O'Connor TG 2000. Resource heterogeneity and ungulate population dynamics. Oikos 89: 383-294.

Irwin LL, Cook JG, McWhirter DE, Smith SG and Arnett EB 1993. Assessing winter dietary quality in bighorn sheep via faecal nitrogen. Journal of Wildlife Management 57: 413-421.

Jenks JA, Soper RB, Lochmiller RL and Leslie DM 1990. Effects of exposure on nitrogen and fibre characteristics of white-tailed deer faeces. Journal of Wildlife Management 54: 389-391.

Karn JF 1997. Phosphorus supplementation of range cows in the Northern Great Plains. Journal of Range Management 50: 2-9.

Kiringe JW, Grudkowwska M and Mbatha KR 1999. Predicting diet habitat quality of Nubian ibex (*Capra ibex nubiana*) using faecal analysis. In: Second Mashav International Course on the Conservation of biodiversity in Desert Ecosystems. Jacob Blaustein International Desert Research Center, Ben Gurion Unbiversity of the Negev, Israel. pp 105-121.

Knapp AK, Blair JM, Briggs JM, Collins SL, Hartnett DC, Johnson LC, and Towne EG 1999. Keystone role of bison in North American tallgrass prairie. Bioscience 49: 39-5.

Kraaij T 2002. Effects of rain, nitrogen, fire and grazing on bush encroachment in semi-arid savanna, South Africa. MSc thesis, University of Stellenbosch, Stellenbosch, South Africa.

Krueger WC 1972. Evaluating animal forage preference. Journal of Range Management 25: 471-475

Leslie MD and Starkey EE 1985. Faecal indices to dietary quality of cervids in old-growth forests. Journal of Wildlife Management 49: 142-146.

Low AB and Rebelo ATG 1998. Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria.

Mbatha KR 2001. The effects of tannin ingestion on the physiology of Boer-goats. MSc Thesis, University of Natal, Pietermaritzburg, South Africa.

McDonald P, Edwards RA, Greenhalgh JFD and Morgan CA. 1996. Animal Nutrition, 5th edn. Longman, U.K.

McDowell LR 1996. Feeding minerals to cattle on pasture. Animal. Feed Science and Technology. 60: 247-271.

Meissner HN, Pieterse E and Potgieter JJ 1996. Seasonal food selection and intake by male impala *Aepyceros melampus* in two habitats. South African Journal of Wildlife Research 26: 56-63.

Milchunas DG, Varnamkhasti AS, Lauenroth WK and Goetz H 1995. Forage quality in relation to long-term grazing history, current-year defoliation, and water resource. Oecologia 101: 366-374.

Milford R and Minson DJ 1965. Determinations of feeding value of pasture and supplementary feeding. Proceedings of the Australian Soociety of Animal Production 6: 319-329.

Mould ED and CT Robbins 1981. Nitrogen metabolism in elk. Journal of Wildlife Management 45: 323-334.

Mueller-Dombois D and Ellenberg H 1974. Aims and Methods of Vegetation Ecology. John Wiley & Sons, New York.

Nelson DW and Sommers LE 1982. Total carbon, organic carbon and organic matter. In: AL Page, RH Miller and DR Keeney (eds.) Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties. American Society of Agronomy, and Soil Science Society of America, Inc. Publisher. Madison, USA. pp 563-571.

Norton BW 1981. Differences between species in forage quality. In: Hacker JB (ed) Nutritional Limits to Animal Production from Pastures. Commonwealth Agricultural Bureaux, Farnham Royal, UK. pp. 89–110.

Owaga ML 1975. The feeding ecology of wildebeest and zebra in Athi-Kaputhei plains. East Africa Wildlife Journal 13: 375-383.

Owen-Smith N and Cooper SM 1987. Palatability of woody plants to browsing ruminants in South African savanna. Ecology 68: 319-331.

Parris R and Child G 1973. The importance of pans to wildlife in the Kalahari and the effects of human settlement on these areas. Journal of South African Wildlife Management Association 3: 1-8.

Reid RL and Horvath DJ 1980.Soil chemistry and mineral problems in farm livestock: A review. Animal Feed Science and Technology 5: 95-167.

Rhoades JD 1982. Soluble salts. In: AL Page, RH Miller and DR Keeney (eds.) Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties. American Society of Agronomy, and Soil Science Society of America, Inc. Publisher. Madison, USA. pp 167-179.

Robbins CT 1993. Wildlife Feeding and Nutrition. Academic Press, London.

Scholes RJ and Walker BH 1993. An African Savanna: Synthesis of the Nylsvley Study. Cambridge University Press, UK.

Shapiro SS, Wilk, MB and Chen HJ 1968. A comparative study of various tests of normality. Journal of the American Statistical Association 63: 1343-1372.

Shipley LA 1999. Grazers and browsers: How digestive morphology affects diet selection. In: KL Launchbaugh, KD Sanders and JC Mosley (eds) "Grazing Behaviour of Livestock and Wildlife" Idabo forest, Wildlife and Range Exp. Sta Bull. No 70, University of Idabo, Moscow, ID. pp 20-27.

Sinclair ARE 1974. The natural regulation of buffalo populations in East Africa. East Africa Wildlife Journal 12: 291-311.

Skinner JD and Smithers RHN 1990. The mammals of the southern African subregion. 2nd edn University of Pretoria, Pretoria, South Africa.

Smet M and Ward D 2005. A comparison of the effects of different rangeland management systems on plant species composition, diversity and vegetation structure in a semi-arid savanna. African Journal of Range and Forage Science 22: 59-71.

StatSoft, Inc. 2002. STATISTICA for Windows [Computer program manual]. Tulsa, OK: StatSoft, Inc, USA.

Stuth JW, Freer M, Dove H and Lyons RK 1999. Nutritional management for free-ranging livestock. In: HG Jung and Fahey GC Jnr (eds). Nutritional Ecology of Herbivores. Proceedings of the Vth International Symposium on the Nutrition of Herbivores, American Society of Animal Science, Savoy, Illinois, USA. pp 696-751.

Underwood JE and Suttle NF 1999. The Mineral Nutrition of Livestock 3rd edn. CAB International,New York.

Vallentine JF 2001. Grazing Management. Academic Press, San Diego.

Van Riet and Louw Landscape Architects and Metaplan 1999. Kimberley Triangle Community Resource Project. The Kimberley Triangle Forum, phases one to seven. Pretoria. 53 pp.

Van Soest PJ 1994. Nutritional Ecology of the Ruminants (2 nd edn). Comstock Publishing Associates, London.

Ward D, Ngairorue BT, Kathena J, Samuels R and Ofran Y 1998. Land degradation is not a necessary outcome of communal pastoralism in arid Namibia. Journal of Arid Environments 40: 357-371.

Ward D, Ngairorue BT, Apollus A and Tjiveze H 2000. Perceptions and realities of land degradation in arid Otjimbingwe, Namibia. Journal of Arid Environments. 45: 337-356.

Wilson JR 1982. Environmental and Nutritional factors affecting herbage quality. In: Hacker JB (ed.). Nutritional Limits to Animal Production from Pastures. Commonwealth Agriculture Bureaux: Farnham Royal, UK. pp 111-131.

Wofford H, Holechek JL Galyean ML, Wallace JD and Cardenas M 1985. Evaluation of faecal indices to predict cattle diet quality. Journal of Range Management 38: 450-454.

Wrench JM, Meissner HH, Grant CC and Casey NH 1996. Environmental factors that affect the concentration of P

and N in faecal samples collected for the determination of nutritional status. Koedoe 39: 1-7.
Wrench JM, Meissner HN and Grant CC 1997. Assessing diet quality of African ungulates from faecal analyses: the effect of forage quality, intake and herbivore species. Koedoe 40: 125-136.
Zacharias PKJ 1986. The use of the cellulase digestion procedure for indexing the dry matter digestibility of forage. Journal of the Grassland Society of Southern Africa 3: 117-121.

Chapter 6

Conclusions and implications for rangeland policy development

Water addition had no effect on grass-nutritional value and aboveground biomass. According to South Africa's National Water Policy and National Water Act No 36 of 1998, water should be protected, conserved, managed and controlled in a sustainable manner because South Africa is largely a dry country with irregular rainfall distribution. Thus, to achieve the sustainable use of water, as it is increasingly becoming the limiting resource in South Africa, the irrigation of ranches, even the smaller ones should not be contemplated as a policy option. Even during drought periods irrigation above the mean annual rainfall is not recommended for improving quality and biomass of grass especially in the semi-arid savanna.

There was more grass biomass and CP and P mass per area in ungrazed plots during the wet season. Nitrogen addition was important, but only during the wet season, probably because of uptake limitation in the dry season. Nitrogen addition is seldom done in South Africa, but may be profitable, especially on smaller ranches. Precautions such as avoiding nitrogen addition near rivers because ammonia may be toxic to fish and limiting eutrophication should be considered if nitrogen fertilizer is applied. These requirements are in line with the National Environmental Management Act No 107 of 1998, National Forests Act No 84 of 1998 and the National Water Act No 36 of 1998 that all control water pollution (e.g., maintaining buffer zones along streams). Ironically, the regulatory requirements of these laws are not holistically communicated to farmers. This requires more interaction between agricultural extension officers and resource users on both commercial and communal rangelands.

In this semi-arid system, fire interacted with nitrogen fertilizer and grazing to improve grass quality. Grazing alone had little effect on grass quality, although in the late wet season, CP and P levels were high on grazed plots. Both fire and grazing remove grass, albeit at different grass ages, resulting in improved nutrition of grass due to the increase of young, actively-growing grass in the sward. The results of this short-term study showed that fire had more positive effects on grass quality than grazing. This supports traditional herders' practise of using fire to destroy unpalatable grass and permit the emergence of palatable re-sprouts. It would be appropriate to recommend that future rangeland policy for South Africa (as South Africa has not got such a policy) should be sensitive to the traditional practise of using fire to improve forage quality. Also, fire has been used to control insect infestation, bush encroachment, selective feeding of palatable plants. Consequently, fire is recommended for consideration in South Africa's rangeland policy as well as in the policies of other African countries that have similar resource use patterns or share agro-ecological conditions with South Africa. However, precautions on when to burn and how frequent should be defined by the vegetation type and rainfall.

Ranching a single animal species is not recommended for sustainable use of the grazing land. It has been observed from the present study that the game ranch, with a wide variety of animal species had low bush encroachment, few poisonous and unpalatable plant species and high plant quality. This is consistent with rangeland usage by African herders who own both cattle and small livestock (e.g., sheep and goats). These animals are herded together. There is a need to sensitize rangeland policy debates to this traditional practise. It would be appropriate for South Africa to examine the rangeland use and management policies of other countries that are sensitive to these kinds of traditional rangeland management.

In contrast, the commercial management type, ranching cattle only, showed the lowest dietary quality of parameters measured, had the highest signs of bush encroachment, and many poisonous and unpalatable plant species (but less than in the communal ranch), all indicating land degradation in spite of rotational grazing and lower stocking density than on the communal ranch (see also Mbatha and Ward in press). Widespread occurrence of bush encroachment has reduced the livestock and game productivity on the range. Our recommendation for the commercially-managed area would be to introduce a greater variety of stock and/or game to reduce selective grazing of certain plant species and its attendant consequences. The communal ranch can also be considered to be degraded, especially close to the inhabited area (see also Smet and Ward 2005). Thus, communal ranchers should be informed about the side effects of high density of grazing animals near homestead. A policy to control the degradation observed closer to the inhabited area is recommended.

Our results also indicate that habitats differ considerably in terms of nutrient quality and susceptibility to degradation. In the Northern Cape, where pans are common, these habitats should be judiciously used to optimise stocking densities because of the high nutrient quality throughout the year. Conversely, our study also showed that ranchers should only lightly stock open savanna habitats in spite of high standing biomass because they may be particularly susceptible to degradation and invasion by poisonous and unpalatable plants. This can be promoted by applying appropriate policy instruments like incentives and disincentives, especially on communal lands (which are *de jure* state properties). Incentives should reward environmentally friendlier behaviour like light stocking and disincentives should discourage heavy stocking. Certain countries (e.g., Namibia) pay drought relief subsidies per cattle head on such open savanna habitats. This has the tendency to encourage dense stocking on systems/habitats whose reproductive capacities might have been exceed. Thus, livestock subsidies that promote recruitment of animals should be discouraged on these habitats.

We recommend that a conservative approach to stocking density be adopted by ranchers. Clearly, using the density estimate that is the lowest for any given season can do this, but this creates problems for ranchers in terms of selling and buying stock to match these estimates. A more pragmatic strategy may involve using the estimate based on P throughout the year because it is lower than that based on either CP or on plant biomass alone (11 of 15 assessments in each case). This difference is especially pronounced at the end of the dry season when pressure on the sward is most extreme. We recognise that this strategy may result in an excess of forage in the wet season. This can be remedied by leasing land to stockowners with limited rangeland available. We recognize that the abovementioned stocking density estimates are short-term in that they are based on current biomass and nutrient values. They further assume that there will be no long-term degradation caused by these stocking densities. Clearly, it would be most appropriate for ranchers to maintain their own annual estimates of biomass and nutrient quality and to adjust their stocking density estimates accordingly. Using a harvest coefficient of 35% for estimating the stocking rate leaves plant residues that will avoid land degradation, allows sustainable use of rangelands and should provide economic returns even during drought.

The negative effects of grazing were more evident in the commercial ranch. In a rotational grazing system, these effects are probably due to returning herds to camps before the plants have had time to recover and, perhaps, due to the use of a single species of livestock, which increases the negative impacts of selective grazing. This problem may be more acute in areas such as this with low and erratic rainfall, which makes it difficult for ranchers to consistently follow a regular rotation of animals among camps. Clearly, ranchers need to follow a more flexible system of rotation and need to examine the state of the sward, moving animals into new camps only once they have recovered sufficiently from the previous period of grazing. The disparities in resource use and rangeland quality in South Africa require the development of a broad or vague framework policy for rangeland management in the country. It ought to be “vague” to allow regions or provinces to further develop this policy to reflect local, provincial or regional realities. For example, in this particular case (Northern Cape), the rangeland policy should focus more on limiting stock numbers both in the communal and commercial sectors. This is a land resource conservation measure (restoration and degradation prevention) and should therefore borrow from the South African LandCare Program. The program requires that livestock grazing, cultivation and harvest of natural resources should be managed in a manner that truncates degradation. This will enhance the long-term productivity and ecological sustainability of South Africa’s limited natural resources and ensure future availability of land resources within the agricultural sector. These would be accomplished if all agricultural land users are facilitated and organized by the Department of Land and Agriculture to utilize the natural resources on which they depend in a sustainable pattern. It should be considered that the formulation of South Africa’s rangeland policy would not start from scratch, but that the existing policies and programs that promote land resource conservation and sustainable utilisation of natural resources could contribute towards it.

It is evident from our study that exclosures are very useful tools for examining the effects of grazing on plant quality and composition. However, in areas such as this, where inter-annual rainfall variation is high, negative effects of grazing are likely to be detected after a number of years (in our case, three years – see also Ward *et al.* 1998, Ward *et al.* 2004). Consequently, we recommend that ranchers use exclosures as medium- to long-term indicators of range condition in semi-arid savannas.

The most surprising finding in this study was that faecal quality was lowest in the commercial management type. We ascribe this to the higher nutrient deposition in communal management (due to higher stocking densities), thereby increasing soil quality, which affects plant quality in turn. This has important implications for the development of “Agrosilvopastoral System”. There is a scope for using this system in the dry parts of South Africa to accommodate multiple needs. In fact, this system is used in woodland or grassland savannas in many parts of the world. The Department of Water Affairs and Forestry (DWAF) strives to kick-start the dissemination and adoption of agroforestry techniques in South Africa and already has a policy to this effect. Also DWAF’s forestry policy and legislation component for “Community Forestry” could be used to implement agrosilvopastoral systems in South Africa’s dry rangelands and farmlands.

An additional factor that may affect this preceding result is that communal animals have freedom of movement and may be better able to access high quality food items. We may interpret this to mean that a continuous grazing system may hold some advantages over a rotational system under these circumstances. If a rotational grazing system is designed such that all paddocks have the same proportional availability of key forage plants the differences we recorded should not occur because animals should be able to access preferred items in each camp. However, if key forage plants are patchily and unevenly distributed among paddocks, then managers may inadvertently be moving their animals to paddocks where lower overall diet quality is achievable. This points to the need for careful selection and distribution of paddocks and timing of movement of animals among paddocks. The high faecal quality of animals in the clay pan habitat with high soil nutrients (see also Smet and Ward 2005, Britz 2004) shows that the pan habitat can be considered a key resource (Illius and O'Connor 2000). Indeed, game numbers in the pan habitat exceed those in other habitats, far in excess of the relative contribution on an area basis. These results demonstrate the importance of strategic planning of paddocks to incorporate this habitat in grazing systems in this region. Overall, our study shows that diet selectivity is a key factor in diet quality in semi-arid savanna. Consequently, assessing plant species availability is not particularly reliable method for assessing either habitat suitability or stocking rates. We recommend that faecal profiling, which explicitly incorporates diet selectivity, may be a more reliable method of managing these habitats.

References

Britz M-L 2004. The effects of soil type and management strategy on vegetation structure and function in a semi-arid savanna, South Africa. MSc thesis, University of Stellenbosch, South Africa.

Illius AW and O’Connor TG 2000. Resource heterogeneity and ungulate population dynamics. Oikos 89: 383-294.

Mbatha KR and D Ward 2006. Determining spatial and temporal variability in quantity and quality of vegetation for estimating the predictable sustainable stocking rate in the semi-arid savanna. African Journal of Range and Forage in press

Smet M and Ward D 2005. A comparison of the effects of different rangeland management systems on plant species composition, diversity and vegetation structure in a semi-arid savanna. African Journal of Range and Forage Science 22: 59-71.

Ward D, Ngairorue BT, Kathena J, Samuels R and Ofran Y 1998. Land degradation is not a necessary outcome of communal pastoralism in arid Namibia. Journal of Arid Environments 40: 357-371.

Ward D, Saltz D and Ngairorue BT. 2004. Spatio-temporal variation and stock management in arid Namibia. Journal. Range Management. 57: 130-140.